

Genetic analysis and selection for weevil resistance in maize

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General abstract

The maize weevil (*Sitophilus zeamais* Motschulsky) is one of the most destructive storage insect pest of maize (*Zea mays* L.) in tropical Africa and worldwide, especially when susceptible varieties are grown. Therefore, grain resistance against the maize weevil should be part of a major component of an integrated maize weevil management strategy. The specific objectives of this study were to: i) determine farmers' perceptions about weevil resistance in maize cultivars; ii) determine the genotypic variation for maize weevil resistance in eastern and southern Africa maize germplasm lines; iii) study the gene action conditioning weevil resistance in the inbred line populations from eastern and southern Africa maize germplasm and to measure their combining ability for yield and weevil resistance; iv) determine the effectiveness of two cycles of modified S_1 recurrent selection in improving a tropical maize population "Longe5" for weevil resistance and agronomic superiority and v) evaluate the effectiveness of the "weevil warehouse techniques" compared to the "laboratory bioassay technique" as methods of maize screening against the maize weevil.

A participatory rural appraisal (PRA) was conducted in three districts between December 2010 and January 2011, to gather information on the maize weevil pest status in Uganda and farmers' perceptions about improved maize varieties and the major attributes desired in new maize varieties. Over 95% of farmers knew the maize weevil and its pest status, and were reportedly controlling the maize weevil using wood ashes, red pepper and *Cupressus sempervirens*. The estimated postharvest weight losses attributed to weevil damage was over 20% within a storage period of four months. The most highly ranked attributes desired in the new maize varieties included high grain yield, tolerance to drought and low nitrogen stresses, resistance to field pests and diseases, good storability and resistance to storage pests.

In the search for new sources of weevil resistance, a total of 180 inbred lines from three different geographical areas were screened for weevil resistance using the laboratory bioassay technique. Eight inbred lines (MV21, MV23, MV75, MV102, MV142, MV154, MV157, and MV170) were consistently grouped in the resistant class, and therefore selected as potential donors for weevil resistance in the maize improvement programs. Large significant genetic variations for weevil resistance, and high levels of heritability (89 – 96%) were observed. The results revealed that there was no significant association between maize weevil resistance and

grain yield; suggesting that breeding for maize weevil resistance can be achieved without compromising grain yield.

Eight weevil resistant and two susceptible inbred line parents were crossed in a 10 x 10 full diallel mating design and the resulting 45 experimental hybrids and their reciprocal crosses evaluated for grain yield and secondary traits under four environments, and also to determine the gene action regulating their expression. The F_1 hybrid seed, F_2 full-sib and F_2 half-sib grain generated from the 45 experimental hybrids and their reciprocals under two environments in Namulonge, were evaluated for weevil resistance using F_1 weevil progeny emergence, median development period (MDP), Dobie's index of susceptibility (DIS), and parental weevil mortality as susceptibility parameters. The general combining ability (GCA), specific combining ability (SCA), and reciprocal effects were all significant for grain yield, with SCA accounting for over 80% of the hybrid sum of squares. Inbred line parent MV44 exhibited positive significant GCA for grain yield and thus can be utilized in the development of synthetics and hybrids. Hybrids MV21 x MV13, MV154 x MV44, and MV154 x MV102 and all hybrids between parent MV142 and the rest of the parental lines exhibited positive and significant SCA effects. For the weevil resistance parameters, the general combining ability (GCA), specific combining ability (SCA) and reciprocal effects were all significant for F_1 weevil progeny emergence, MDP, and DIS in the three seed categories. The results revealed that weevil resistance was governed by additive gene action, non-additive, and maternal effects. Parents MV170 and MV142 were consistently exhibiting weevil resistance in the three seed categories and thus recommended for future breeding strategies. Furthermore, most of the hybrids generated from parental line M142 were noted to exhibit outstanding performance in terms of grain yield and weevil resistance.

Another study was conducted to determine the effectiveness of two cycles of modified S_1 recurrent selection towards the improvement of weevil resistance in a maize population Longe5. Over 540 selfed ears were selected from the source population (C_0) and screened for weevil resistance in the laboratory at Namulonge. Based on weevil resistance characteristics, 162 genotypes were selected from C_0 and recombined in an isolated field to generate cycle C_1 . The same procedure was used for generating cycle C_2 from cycle C_1 , but instead 190 weevil resistant C_1 genotypes were selected and recombined to form C_2 . Seed from cycles C_1 and C_2 , together with that from the source population (C_0), was used to plant an evaluation trial in three locations, to compare the performance of the three cycles in terms of grain yield and reaction to the major foliar diseases, and also to produce seed for subsequent screening against weevil

infestation. A total of 54 seed samples were screened for weevil resistance in a laboratory at Namulonge, in an experiment laid out in a randomized complete block design. A reduction in grain weight loss of 65% was registered in the C₂ seed, whereas in C₁ seed it was 15%. A similar trend was observed for F₁ weevil progeny emergence and grain damage. Grain yield results indicated a yield gain of 19% realized from cycle C₂ while a yield gain of 7% was realized from cycle C₁. Furthermore, reductions in disease severity of 27%, 10% and 13% were exhibited for *Turcicum* leaf blight (TLB), grey leaf spot (GLS) and rust disease, respectively in cycle C₂. The results indicated that Longe5 can be improved for maize weevil resistance, grain yield, and resistance to foliar diseases through selection. Further recurrent selection cycles would be recommended.

The last study was aimed at evaluating the potential of shelled grain and suspended ear options of the weevil warehouse technique in discriminating maize genotypes into different susceptibility classes, based on genotype response to weevil attack. It involved comparing the effectiveness of the two options under the weevil warehouse technique with the laboratory bioassay technique using grain damage and grain weight loss as the maize grain susceptibility parameters. Fourteen maize genotypes were screened using the weevil warehouse and the laboratory bioassay techniques at Namulonge. On grouping the 14 genotypes into different response classes, high levels of consistency were observed in the three screening techniques. Therefore, the two weevil warehouse screening options being faster and effective in discriminating maize cultivars towards weevil attack, they were found to be better than the laboratory bioassay technique. The minimum evaluation period required to discriminate genotypes by the two weevil warehouse options was two months from the onset of the experiment.

The maize weevil was noted to be an important storage pest constraining maize production in Uganda. The major weevil control measures included proper postharvest handling procedures and use of indigenous technical knowledge. The results also revealed that host plant resistance could significantly reduce grain damage. It was further revealed that grain resistance against the maize weevil could be enhanced through hybridization and recurrent selection; thus the germplasm identified in the study can provide new sources of maize weevil resistance for commercial deployment and further breeding.

Declaration

I, **Lwanga Charles Kasozi**, declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
3. This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons.
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Signed.....Date.....

Lwanga Charles Kasozi

As the candidate's supervisors, we agree to the submission of this thesis:

Signed.....Date.....

Prof. John Derera (Principal supervisor)

Signed.....Date.....

Prof. Pangirayi Tongoona (Co-supervisor)

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Dedication

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Introduction to the thesis

1 Importance of maize

Maize (*Zea mays* L.) is one of the most widely grown crops worldwide, with different germplasm adapted to various environmental conditions including temperate, tropical and sub-tropical zones (Koutsika-Sotiriou, 1999). Globally, maize is ranked third, after wheat and rice, in terms of volume produced and importance (FAO, 2006). The estimated area under maize production worldwide is 170,398,070 hectares, with an average yield of 5.184 t ha⁻¹. In Africa the area under maize production is 34,549,888 hectares, with an average yield of 1.882 t ha⁻¹. In eastern Africa the area under maize production is 15,130,956 hectares, with an average yield of 1.729 t ha⁻¹. In Uganda the area under maize production is 1,063,000 hectares with an average yield of 2.399 t ha⁻¹ (FAOSTAT, 2010).

In Uganda maize is the most widely adapted crop cultivated in all agro-ecological zones of the country, with over 57% of the farming households engaged in its production (Haggblade and Dewina, 2010). A larger proportion of maize is grown in the mid-altitude zones covering central, mid-western and mid- eastern districts, and highland zones covering the eastern districts of Uganda. Production in the mid-altitude zones accounts for 70%, while that in highland zones accounts for 30% of total maize production in Uganda (Kikafunda et al., 2001). Regarding its dietary contribution, maize is the third most important staple food crop in Uganda providing up to 11% of the country's caloric requirements, compared to 13% and 18% provided by cassava and bananas, respectively (FAO, 2009). Maize is widely consumed throughout Uganda and is a major ingredient in livestock and poultry feeds. The maize stover is on the other hand used as fuel in form of firewood and as mulch in banana and coffee plantations (Bigirwa et al., 2001).

Countrywide, maize has increased its importance as a regular source of income for a number of individuals engaged in its production and trade in Uganda (Ferris et al., 2006). Maize is increasingly becoming an important cash crop in Uganda, as its value on the eastern African regional market has appreciated due to the persistent food shortage in the region arising from erratic weather patterns and political instability (Magnay, 2004). This was reflected in the annual maize exports in Uganda for the period between 2005 and 2007 when over 167,000 tons were

sold to the east African regional market (Benson et al., 2008). Consequently, Uganda earned over US\$24 million from maize exports (Okoboi, 2010).

In spite of its great importance in Uganda, maize productivity is still low with yields as low as 2.399 t ha⁻¹ that are far below its yield potential, documented at 9.59 t ha⁻¹, in USA (FAOSTAT, 2010) and up to 7.00 t ha⁻¹ in Uganda as on-station yield. Various production constraints are being blamed for the wide gap between on-station and on-farm yields. These constraints are broadly grouped into abiotic, biotic and socio-economic factors.

2 Production constraints

The major abiotic factors constraining maize production are soil nutrient deficiencies, especially of nitrogen, phosphorous and potassium which maize require in adequate quantities for proper establishment and growth (Kochhar, 1981); and drought-stress, all of which are escalated by climate change and environmental degradation, as more marginal land is put to crop production (Bänziger and Diallo, 2001). The poor maize yields are attributed to drought which is persistently becoming a serious production constraint, as a result of the major changes in climate resulting in erratic rainfall distribution in Uganda (Komutunga and Musiitwa, 2001; Makuma-Massa et al. 2012). Some progress is being registered regarding the development of nitrogen- and drought-stress maize cultivars adaptable to tropical conditions (Makumbi et al. 2011).

Regarding the socio-economic factors hindering the enhancement of maize productivity, limited farmer knowledge and access to modern production technologies stand out as key constraints to maize productivity. Despite the reasonable number of maize cultivars and appropriate agronomic packages developed, there are still low adoption rates at farmer level. Sserunkuuma (2003) noted that high capital inputs, including improved seed, fertilizers and herbicides, to be among the major socio-economic constraints. In similar regard, (Bigirwa et al., 2005) observed that development of stress-tolerant maize varieties ought to be more sustainable particularly at smallholder farmer level where the technology can only be utilized in the seed. However, the need to assess farmers' knowledge and access to the improved maize production technologies would be crucial for verifying technology appropriateness and acceptability.

The biotic factors constraining maize production include: foliar diseases, ear and stalk rots, field and postharvest pests. Among the biotic constraints, postharvest pests have not received adequate attention yet they cause devastating yield and quality losses. The major insect pests hindering maize production in Uganda are stem borers, mainly, *Busseola fusca* and *Chilo partellus* (Kalule et al., 2006), and termites (*Macrotermes* spp.). On the other hand, the maize weevil (*Sitophilus zeamais* Mostchulsky) is the most important postharvest pest in Uganda causing tremendous losses in quantity and quality of maize under storage. However, losses in grain quantity and quality associated with weevil infestation is not clearly documented in Uganda, but in other sub-Saharan African countries the loss in grain weight attributed to weevil damage exceeds 13% (Giga et al., 1991; Ngatia and Kimondo, 2011). Nevertheless, the moderate temperatures ($25\pm 5^{\circ}\text{C}$) and the relative humidity above 50% exhibited throughout the year in most maize growing areas of Uganda ought to accelerate weevil multiplication and ultimately severe damage of the grain under storage. Similarly, Tefera et al. (2010) reported temperatures of $28\pm 2^{\circ}\text{C}$ and relative humidity of $65\pm 5\%$ to be conducive for weevil rearing (growth and multiplication).

In spite of the increasing weevil prevalence countrywide, there is scanty information on farmers' knowledge about weevils, their economic importance, coping methods, the possibility of resistance and significance of resistant cultivars, if any. Documentation of such information raises awareness and ultimately enhances weevil control. Consequently, a participatory rural appraisal was conducted in representative districts of the major maize growing zones of Uganda, to capture information on the significance of the maize weevil in addition to other production related issues.

Demisse et al. (2008) indicated that grain infestation by the weevil usually begins in the field before grain harvesting and subsequently weevils multiply within the grain and cause substantive damage under storage. Thus warranting control measures that are effective both in the field level and under storage. Grain resistance against weevil infestation ought to be a sustainable control measure in this regard. Genetic variability for weevil resistance has been reported in various maize germplasm including improved, partially improved and local landraces (Kossou et al., 1993; Siwale et al., 2009). Different sources of genetic variability for weevil resistance in maize germplasm from different geographical locations would be valuable in devising appropriate weevil control measures in addition to selecting potential parents for subsequent studies.

Information on combining ability and/or gene action, and heritability for weevil resistance in adaptable maize germplasm in Uganda would also be very vital in designing breeding strategies. Therefore, screening of germplasm from different geographical locations would enhance the genetic diversity towards weevil resistance. The study materials comprise of both tropical and subtropical maize germplasm obtained from eastern and southern Africa, respectively, for screening for weevil resistance and studies on combining ability, gene action and heritability.

On the other hand, maize screening against weevils requires a fast, precise and cheap protocol that can effectively discriminate genotypes into different response classes. Dobie (1974) developed a popular screening protocol that effectively discriminates maize germplasm using the susceptibility index (SI). However, the Dobie (1974) procedure is expensive as it requires a lot of time and labour. Based on these limitations, a cheap, fast and precise maize screening protocol would provide an alternative to the Dobie (1974) procedure. For that reason, the weevil warehouse technique that employs the “free choice” maize screening procedure should be compared to the “no-choice” laboratory procedure (laboratory bioassay) for effectiveness in discriminating maize genotypes towards weevil infestation and damage.

Results from previous research on the genetics of weevil resistance in maize indicate that resistance is governed by both additive and non-additive gene action (García-Lara et al., 2009; Dari et al., 2010). The influence of additive genes would imply that maize resistance against weevils could be enhanced through selection. Hence, investigations on the effectiveness of recurrent selection in improving weevil resistance in one of the maize populations would add more knowledge on the subject. This study used weevil susceptible Longe5, as one of the most popular open pollinated maize varieties in Uganda, to determine the effectiveness of S_1 modified recurrent selection in improving Longe5 for weevil resistance. Due to time constraint some modifications were made on the frequency of selfing, to only once at the beginning of the selection process.

3 Justification for the study

The MW is an inherent production constraint encountered in all maize growing regions of Uganda causing significant grain weight losses under storage. The MW negative impacts on the grain are further felt by it being a primary pest, paving way for secondary infections by molds (ear rot pathogens) which lead to further deterioration in grain quality in addition to accumulation

of aflatoxins and mycotoxins (Sone, 2001; Kaaya et al., 2005). With the growing local and regional market for maize, it is imperative to provide an urgent remedy to the maize weevil problem in Uganda. Development of maize weevil resistant germplasm provides an appropriate and sustainable remedy to the weevil problem in maize (Dobie, 1977; Bergvinson, 2001).

4 Study objectives

4.1 Broad objective

Development and adoption of maize weevil resistant maize varieties can provide a cheap and sustainable remedy to the deteriorating maize grain quality storability in Uganda. The overall objective of the study was to minimize postharvest yield losses associated with storage weevils through development of high yielding adaptable maize varieties that are resistant to the maize weevil and other major biotic constraints for the benefit of all players in the maize value chain in Uganda.

4.2 Specific objectives

The specific objectives were to:

- i. Determine farmers' perceptions about weevil resistance in maize cultivars;
- ii. Determine the genotypic variation for maize weevil resistance in eastern and southern Africa maize germplasm lines;
- iii. Study the gene action conditioning weevil resistance in the inbred line populations from eastern and southern Africa maize germplasm and to measure their combining ability for yield and weevil resistance;
- iv. Determine the effectiveness of two cycles of modified S_1 recurrent selection in improving a tropical maize population "Longe5" for weevil resistance and agronomic superiority.
- v. Evaluate the effectiveness of the "weevil warehouse technique" compared to the "laboratory bioassay technique" as methods for screening maize against the maize weevil.

4.3 Hypotheses

The research hypotheses were as follows:

- i. Farmers are aware of the damages caused by the maize weevil on the maize grain during storage and believe that grain damage can be minimized through cultivation of weevil resistant maize varieties;
- ii. Maize germplasm from eastern and southern Africa exhibit genotypic variations in weevil resistance, therefore effective sources of resistance can be found and used for breeding new weevil resistant varieties;
- iii. Weevil resistance in maize germplasm from eastern and southern Africa is controlled by genes with additive gene effects hence it can be improved through selection; and there is good specific combining ability for both yield and weevil resistance in the inbred line populations that would be exploited in designing hybrids and synthetic populations.
- iv. The tropical maize population Longe5 can be improved for weevil resistance and agronomic superiority through modified S_1 recurrent selection.
- v. There are no differences between the effectiveness of the “weevil warehouse technique” and the “laboratory bioassay technique” in screening maize germplasm for weevil resistance; and each technique can effectively discriminate maize germplasm into different response classes without losing experimental precision.

5 Structure of thesis

This thesis is structured in such a way that literature review, activities and results of each of the five objectives, overview and future directions are each presented as separate chapters.

The structure of the thesis is as indicated below:

1. Introduction to thesis;
2. Chapter one: Literature review;
3. Chapter two: Farmers' perceptions about the need for weevil resistant maize cultivars;
4. Chapter three: Genotypic variation for maize weevil resistance in genetic backgrounds from eastern and southern Africa;

5. Chapter four: Diallel analysis of maize weevil resistance in eastern and southern Africa maize germplasm lines;
6. Chapter five: Diallel analysis of yield in eastern and southern Africa maize germplasm lines;
7. Chapter six: Response of “Longe5” to two cycles of modified S₁ recurrent selection for maize weevil resistance and agronomic superiority;
8. Chapter seven: The effectiveness of the “weevil warehouse” and “laboratory bioassay” as techniques for screening maize genotypes for weevil resistance; and
9. Chapter eight: General overview and future directions

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Chapter One

Literature review

1.1 Introduction

This literature review gives the general perspective of maize production constraints and the interventions made to control the various constraints. More emphasis is given to the maize weevil, which is the most economically important storage pest in Uganda and beyond. Some highlights have been made on the foliar diseases in Uganda, particularly *Turcicum* leaf blight (TLB), grey leaf spot (GLS), and common rust although it still has very scanty information. The main areas reviewed include the significance of the maize weevil, its biology and infestation process, genetic variability in weevil resistance, screening and breeding for weevil resistance, combining ability and gene action conditioning weevil resistance.

1.2 The maize weevil and its biology

The maize weevil, *Sitophilus zeamais* Motschulsky, is a small black beetle of length ranging from 2.5 mm to 4.5 mm. Its head is protruded into a long snout or proboscis, with elbowed antennae. Its wing covers (elytra) are marked with four reddish-brown spots (Khare, 1994). The maize weevil belongs to the Kingdom-*Animalia*, Phylum-*Arthropoda*, Class-*Insecta*, Order-*Coleoptera*, Family-*Curculionidae*, Genus-*Sitophilus*, and Species-*zeamais*. The maize weevil is usually prevalent in the warm humid zones worldwide, especially in the tropics and sub-tropics where maize is commonly grown. The female uses the snout to bore the grain into which a hole is made where it lays eggs. Its eggs are white oval and usually covered with a waxy secretion that forms a plug. One female weevil can lay up 400 eggs in its lifetime and this explains their rapid population growth. The egg develops into white limbless larvae that later pupate within the grain. In the maize grain, weevils complete their full development cycle, from egg to adult, within a period of 28 days in susceptible cultivars to 64 days in resistant cultivars at a temperature of $30\pm 2^{\circ}\text{C}$ and grain moisture content of $13\pm 2\%$. The optimum temperature and relative humidity required for weevil breeding and growth are $28\pm 2^{\circ}\text{C}$ and $70\pm 5\%$, respectively (Tefera et al., 2010). Walgenbach et al. (1987) reported the average period required for an adult weevil to begin mating to be three days. The maize weevil can survive up to one year, with an average

life span ranging from four to seven months (Kranz et al., 1997). Knowledge of the maize weevil biology can enhance selection of appropriate control strategies.

The maize weevil is reported to thrive well within a temperature range of $22\pm 2^{\circ}\text{C}$ and $29\pm 2^{\circ}\text{C}$, weevil activities are lowered by temperatures outside this range; death can even occur at temperatures below 15°C and above 36°C (Barney et al., 1991). Consequently, conditions for mass weevil rearing were also optimized within the same temperature range (Tefera et al., 2010). Another factor responsible for the high weevil prevalence, especially, in the field is the high grain moisture content which is usually above 15% reported to be conducive for weevil attack, as opposed to the lower moisture content $<13\%$ usually exhibited during storage (CIMMYT, 2001b). Another weather parameter influencing weevil activity is relative humidity; the range between 50 and 70% promotes weevil growth and reproduction, while relative humidity below 50% reduces the two processes (Okelana and Osuji, 1985). Therefore, physical control measures may exploit conditions outside the optimum activity range to enhance their effectiveness.

1.3 Significance of the maize weevil in maize production

The maize weevil is usually prevalent under warm and humid conditions (Barney et al., 1991; CIMMYT, 2001b); these conditions are mostly manifested under tropical and sub-tropical climate. Thus the maize weevil is a serious storage insect pest encountered by a number of farmers, particularly small scale farmers growing maize under such environments. It mainly attacks maize, sorghum, rice, and to a less extent wheat, but it is not found on wild plants (Giles and Ashman, 1971). Hence, a fairly narrow host range of the maize weevil can better the opportunities for its control. Several reports have highlighted the complex losses associated with the maize weevil including weight and quality losses in addition to accumulation of mycotoxins (Barney et al., 1991; Sone, 2001; Kaaya et al., 2005). Sone (2001) reported more infections with *Aspergillus flavus*, *A. candidus*, and *A. terreus* in the maize grain damaged by the maize weevil than in intact grains. These results indicate that weevils are responsible for secondary grain infection by ear rot fungi. Therefore, grain losses encountered as a result of weevil infestation may exhibit double deterioration both in quantity and quality.

1.4 Maize infestation by the maize weevil

The maize weevil usually begins infestations when the crop is still in the field just before harvesting (Demissie et al., 2008). The first line of resistance to weevil attack is to minimize grain infestation in the field. Thus, tight husk covers play a vital role as the main physical barrier to weevil attack is the husk cover. Genotypes with tight husks covering the ear up to the tip prohibit weevil genotype into the ear, as opposed to ears with loose husks that permit free weevil genotype into the ear (Giles and Ashman, 1971).

The role of husk covers in protecting the maize ears has been demonstrated in various studies. For example, Ajibola (1971) observed more weevils in the maize crop in Nigeria when the husk tips had begun opening than when they were still intact. Similarly, Giles and Ashman (1971) indicated that more infestations were encountered in open ears and ears with loose husk covers than in ears with tight husk covers in Kenya. Demisse et al. (2008) observed that even resistant maize genotypes with loose husk covers were also prone to weevil attack in the field. These observations emphasize the role of husk cover in protecting maize ears against maize weevil infestations in the field. Grain protection by husk cover was also reported during storage, whereby husked ears promoted fewer weevils and ultimately encountered less damage than de-husked and/or shelled maize (Kossou et al., 1992).

Grain moisture content is another factor known to affect field infestation by the maize weevil. Giles and Ashman (1971) reported increased weevil prevalence towards grain maturity and the beginning of drying, when grain moisture content drops to a range between 60% and 13%. Therefore, measures targeting at minimizing grain infestation at both field and storage levels should be promoted, as they are expected to maintain low weevil populations in the grain. Proper sanitation, especially, during postharvest handling (including storage) is a critical weevil control point, that if weevils are minimized during the process, their growth cycle would be negatively affected. Subsequently, infestations originating from remnant grains in stores can be reduced in grain in the field and during storage, and this may lead to minimal weevil attack in the new grain stock.

1.4.1 Effect of maize storage forms and conditions on grain infestation

Grain handling plays a major role in the final quality of maize produce (Barney et al., 1991). Grain moisture content is one of the key factors to consider during storage. Grain that is

properly dried to moisture content $\leq 11\%$ would encounter minimal weevil infestation as opposed to higher moisture content (Tefera et al., 2011). On the other hand, the form in which grain is stored also influences the extent of grain damage; Kossou et al. (1992) reported lower weevil attack in maize stored in husked form than to the one stored as dehusked cobs or shelled grain. However, maize storage in husked or dehusked form is only limited to subsistence scale of maize production, as it is not practically possible under large scale maize production. Another set of conditions determining storage effectiveness and thus grain quality maintenance and longevity are temperature (Ileleji et al., 2007) and relative humidity (Okelana and Osuji, 1985). Therefore, grain manipulation as regards to storage form and conditions determines its storability.

1.5 Weevil resistance mechanisms

Naturally plants have in place barriers which protect/minimize detrimental effects from foreign organisms or stress conditions. These barriers may be physical and thus directly blocks plant attack by a pest or a disease pathogen by physical means; or they may be biochemical and thus their reactions are triggered by invasion of the plant and/or plant part.

The physical mechanisms (characteristics) of the ears and grains include: tight husks covering the ears up to the tips (Giles and Ashman, 1971) and thick strong pericarp for seeds (García-Lara et al., 2004). A number of studies have been conducted on kernel characteristics such as grain surface relief, kernel size and hardness, and pericarp thickness (Tipping et al., 1988; Gudrups et al., 2001; García-Lara et al., 2004); all of which were reported to affect grain attack and ultimately damage by weevils. Tipping et al. (1988) conducted studies on grain surface relief and reported more damage in kernels with rough grain surfaces than those with smooth ones. They attributed this incidence on the firm grip by the maize weevil easily achievable on the rough surfaces as compared to smooth ones. These findings reveal the need to promote cultivars with smooth kernels. Probably shiny flint-kernelled cultivars could exhibit this characteristic as compared to the rough surfaced dent ones. Regarding kernel size, Gudrups et al. (2001) reported higher weevil resistance in large sized kernels than in the small sized ones. On the other hand, a high proportion of pericarp to whole grain was observed in weevil resistant maize cultivars and was associated with high proportions of diferulic acids and hydroxyproline-rich glycoproteins that are reported to enhance grain hardness (Garcia-Lara et al., 2004).

Regarding bio-chemical weevil control mechanisms, antibiosis occupies a key position. When the maize weevil gains access to the grain, variations in responses against its damaging effects have been observed; with some maize genotypes permitting more prominent activities, while in others it is minimal. Derera et al. (2001) reported antibiosis, as one of the mechanisms responsible for hindering weevils from fully manifesting pest activities such as, feeding/damage, growth, and reproduction. Other effects of antibiosis include increased weevil growth and development periods, reduced weevil size, and juvenile and/or adult mortality. Several biochemical substances are responsible for antibiosis among them are enzymes especially peroxidases and phenolic compounds particularly simple phenolic acids, diferulic acids, hydroxyproline-rich glycoproteins, p-coumaric acid, and E-ferulic acids (Garcia-Lara et al., 2007). These compounds responsible for antibiosis have been reported in higher concentrations in weevil resistant maize genotypes than in susceptible ones (Classen et al., 1990; Arnason et al., 1997; García-Lara et al., 2007). Classen et al. (1990) reported higher phenolic acid content in the pericarp and aleurone layers of weevil resistant maize germplasm than in susceptible one. Results from related studies have also revealed the occurrence of phenolic acids in the embryo, in addition to the aleurone layer and the pericarp (Arnason et al., 1997). Conversely, higher levels of soluble peroxidase enzymes were found in the endosperm of weevil resistant maize (Garcia-Lara et al., 2007). Figueira et al. (2003) reported the occurrence of hydrophobic amylase inhibitors in maize resistant to *Fusarium* ear rot and insects (weevils inclusive). Knowledge of the physical, biochemical and other resistance mechanisms enriches the basis for enhancing weevil control measures, especially the breeding strategies which ought to capitalize on these mechanisms when improving maize germplasm for weevil resistance.

1.6 Weevil control measures

The maize weevil, *S. zeamais*, is a very aggressive insect that if not timely contained, may cause enormous grain losses both quantitatively and qualitatively. Various weevil control measures have been tested, some of them like tight husk cover and general sanitation have been deployed at farmer level (Ajibola, 1971; Giles and Ashman, 1971; Kossou et al., 1992), while others such as botanical extracts (Nerio et al., 2009; Paes et al., 2012) and biological control agents (Adane et al., 1996) are still at experimentation stages. Measures like general sanitation that may entail cultural control methods (Barney et al., 1991), tight husk covers and low grain moisture content (<13%) target at minimizing grain infestation and thus provide the first line of control measures, while host plant resistance (due to antibiosis and other resistance

mechanisms) aims at minimizing weevil populations in the grain after infestation has occurred (Derera et al., 2001), and hence serves as a second round of grain protection against weevil damage. The physical and biochemical control measures have already been discussed under weevil resistance mechanisms. Therefore, other weevil control measures like proper sanitation, hermetic storage system, use of chemicals, biological control agents, botanical extracts and host plant resistance are discussed in this section.

1.6.1 Sanitation

Ensuring crop and grain sanitation is a key step for effective weevil control strategies, elimination of maize ears in the fields and storage facilities breaks the weevil development cycle. Infestation arising from infested remnant cobs in the field are quite minimal, as most weevils die before the next maize crop is old enough for attack, therefore, the major source of weevil infestations is the infested maize stock/residues during storage (Giles and Ashman, 1971). This observation was further highlighted by Ajibola (1971) who observed weevils in flight in the field of the maize crop, thereby confirming the incidence of infestations from the remnant grains in stores/granaries. Thus, it is always necessary to clean (and if possible apply insecticides/fumigate) grain storage facilities between different crop harvests and storage. The simplicity and practicability of grain sanitation makes it the most popular weevil control measure, affordable by all categories of farmers and can effectively complement other control measures.

1.6.2 Hermetic storage system

As the name suggests, weevil control using hermetic storage conditions deprive the weevils of the oxygen and thus they ultimately die of suffocation. Hermetic storage system has been reported to be effective, easy and safe due to its freedom from chemicals (Yakubu et al., 2011). The most commonly used hermetic storage materials are super grain bags and metal silos (De Groote et al., 2013). Hermetic storage would be an appropriate weevil control measure to both smallholder and large scale farmers; however, the high initial capital requirement may be prohibitive to smallholder farmers who are usually constrained by finances.

1.6.3 Chemicals

Chemicals control insects directly either through stomach poisoning, or by interfering with their nervous system, or indirectly as protectants restricting grain infestation. The use of commercial

chemicals, especially, organophosphate-pyrethroid combinations such as pirimiphosmethyl and permethrin, is among the common practices being adopted in eastern and southern Africa. Malathion is also a commonly used contact insecticide for prevention and/or elimination of weevil infestation in the grain. However, studies by Mutiro et al. (1992) and Perez-Mendoza (1999) demonstrated resistance by *S. zeamais* to malathion and other chemicals. Thus, its usage may as well be minimized in Uganda. Phosphides, usually supplied as Aluminium-phosphide or Zinc-phosphide, are also commonly used for fumigation purposes under air-tight conditions during storage. Nevertheless, the use of chemicals for control of the maize weevil has many challenges including their prohibitive prices, human and animal health hazards arising from their toxicological nature and through their abuse, in addition to their persistence in the environment. Furthermore, development of insecticide resistance by the maize weevil renders chemical control measures less effective and ultimately more expensive in addition to being unsafe (Giles and Ashman, 1971; Oliveira et al., 2007; Braga et al., 2011; Corrêa et al., 2011).

1.6.4 Biological control agents

Considering the many disadvantages associated with chemical control against *S. zeamais*, effective, cheap alternative control measures that ought to be user- and environmentally-friendly, needs to be explored. Deployment of biological control measures is one promising area that needs further exploration for effecting maize weevil control. Like for a number of other insect pests, *S. zeamais* is affected by natural enemies (entomo-pathogenic micro-organisms), particularly fungal endophytes and/or exophytes that exhibit high potential to control pest populations to minimum levels. The major natural enemies controlling weevil populations include: *Fusarium* species and *Beuaveria* species, especially *F. verticilloides* and *B. bassiana*, respectively (Adane et al., 1996). Some success have been registered with five isolates of *B. bassiana* whose effectiveness towards suppressing *S. zeamais* and reducing weevil damage during storage was not significantly different from chemical control (Adane et al., 1996). However, use of *F. verticilloides* as a biological control agent may not be feasible for weevil control strategies as it is also a plant pathogenic fungus (Bigirwa et al., 2007). Other categories of natural enemies reported in the control of the maize weevil include parasitoids (Flinn et al., 2006; Chaisaeng et al., 2010) and predators (Schöller and Flinn, 2000).

1.6.5 Botanicals

Another alternative control measure with a high potential in controlling the maize weevil particularly during storage are plant parts either used directly, or in form of powders and/or liquid extracts commonly known as botanical extracts. The efficacy of botanical extracts from various plant species have been reported towards effective control against *S. zeamais* during storage (Nerio et al., 2009; Mao and Henderson, 2010; Paes et al., 2012; Ukeh et al., 2012). Nerio et al. (2009) isolated essential oils from leaves, stems and flowers of *Lippia* spp., *Tagetes* spp., *Rosmarinus* spp., *Cananga* spp., *Eucalyptus* spp. and *Cymbopogon citratus* in Columbia and were successful in repelling maize weevils from the study samples. Other successful studies on the effectiveness of botanical extracts in the control of the maize weevil were registered in mustard essential oil in Brazil and *Aframomum melegueta*, and *Zingiber officinale* in Nigeria (Paes et al., 2012; Ukeh et al., 2012). The success registered from these studies manifests the high potential of botanicals as alternatives to commercial chemical use for weevil control. Hence, they have practical implications, especially to small scale farmers with limited access to commercial synthetic pesticides, but with easy access to such botanicals. Additionally, use of botanical extracts would complement other weevil control measures such as host plant resistance. It also provides an opportunity for further exploration and validation of indigenous technical knowledge which ought to enrich the knowledge base. Results from the current participatory rural appraisal indicated that botanicals such as leaves of *Cupressus* spp. were being introduced to the maize grain for purposes of repelling the maize weevil.

1.6.6 Use of inert materials

Inert substances such as wood ashes, diatomaceous earth silicosec and mineral industrial filter cakes have demonstrated good levels of effectiveness towards controlling the maize weevil. Demissie et al. (2008) separately used these substances in Ethiopia and observed an increase in weevil death. Up to 100% weevil mortality was registered within 15 days after use of diatomaceous earth silicosec and mineral industrial filter cakes. Another substance reported to be effective against weevils during storage is spinosad (Athanasios et al., 2008). Spinosad is based on the metabolites from a fungus, *Saccharopolyspora spinosa* (actinomycete), with low mammalian toxicity but effective against insect pests by affecting their nervous system, through ingestion or by contact (Subramanyam et al., 2007).

1.6.7 Host plant resistance

Host plant resistance in this context is the ability of the grain to restrain weevil attack. Host plant resistance technology is embedded in the seed and thus may not warrant extra costs to the farmer when acquiring appropriate seed. Consequently, host plant is one of the most sustainable components of integrated pest management strategy, especially at small scale farmer level with limited capacity to invest in chemicals for weevil control, in addition to other agro-inputs. Resistance to maize weevil has been reported by various researchers (Serratos et al., 1993; Abebe et al., 2009; García-Lara et al., 2009; Dari et al., 2010). Serratos et al. (1993) used grain damage and F₁ progeny emergence, and observed more resistance in the segregating populations derived from weevil resistant pool 15 QPM as compared to those derived from the susceptible pool 34 QPM in Mexico.

Abebe et al. (2009) identified a resistant maize variety (BHQP-542) among twelve moderately resistant varieties screened for weevil resistance in Ethiopia. García-Lara et al. (2009) genotyped 163 F₂ populations derived from a resistant and susceptible parent in Mexico, and mapped QTLs associated with weevil resistance parameters. On the other hand, Dari et al. (2010) reported resistance among S₁, S₂, S₃ and S₄ populations against weevils and used the same populations for heritability studies in their single cross hybrids in Zimbabwe.

1.7 Genetic variation for weevil resistance

Genetic variability refers to the different levels exhibited in the expression of a trait(s) among diverse genotypes. Some genotypes may express traits in high magnitudes; some individuals may exhibit moderate expression, while others may exhibit low gene frequencies for particular traits. Therefore, genetic variability enables selection of genotypes with a desired frequency of alleles for specific traits of interest, and provides an opportunity for improving genotypes with low trait expression to desirable levels.

Regarding maize resistance to weevil infestation, foregoing research reveals that maize exhibits genetic variation for weevil resistance in a number of resistance parameters (Kim and Kossou, 2003; Siwale et al., 2009; Temesgen and Waktole, 2013). Kim and Kossou (2003) reported wide genetic diversity among 20 open pollinated varieties and 144 experimental hybrids from screening trials in Benin and were able to identify germplasm for subsequent weevil improvement programs. In Zambia, Siwale et al. (2009) screened 50 improved maize cultivars

from CIMMYT-Harare and two local landraces and observed significant genotypic variation among the test cultivars. In Ethiopia, Abebe et al. (2009) screened 13 improved maize varieties and were able to classify them into resistant and moderately resistant categories. They further reported differences in the effectiveness of resistance parameters particularly, the median development time, F_1 progeny emergence; percent seed damage and seed weight loss in discriminating maize genotypes into different response classes. García-Lara et al. (2009) reported genetic variability in 163 F_2 progenies derived from a cross between weevil susceptible and weevil resistant maize genotypes. In related studies, Dari et al. (2010) also reported significant genotypic variations for maize weevil resistance among S_1 , S_2 , S_3 , and S_4 inbreeding populations used for correlating weevil resistance between inbred line parents and their single cross hybrids. The genetic variability reported from all studies demonstrates the high potential for germplasm exploitation in the quest for improving maize against weevil damage.

1.8 Screening maize genotypes against the maize weevil

Identification of weevil resistant germplasm for use in the breeding process requires a robust method that can effectively discriminate resistant and susceptible genotypes. Screening requires a cheap and fast method that can precisely classify maize germplasm into appropriate response categories namely resistant, moderately resistant, moderately susceptible and susceptible. Discrimination of cultivars involves utilization of resistance parameters to guide the process. The resistance parameters commonly used for discriminating maize genotypes towards response to weevil infestations include: grain hardness, grain weight, grain size, grain damage, parental weevil mortality, number of F_1 weevil progenies that emerge, median development period, period to F_1 weevil progeny appearance, pericarp thickness, protein and phenolic compound content (Widstrom et al., 1972; Dobie, 1974; Garcia-Lara et al., 2004; Garcia-Lara et al., 2007). Significant correlations have been reported between the aforementioned parameters and weevil resistance (Widstrom et al., 1972; Garcia-Lara et al., 2004; Abebe et al., 2009; Siwale et al., 2009).

One or more weevil resistance parameter(s) may be required to select the right germplasm with a high frequency of desired alleles. This is very crucial towards maximizing genetic gain during germplasm improvement for weevil resistance. Since it may not be possible to visually identify weevil resistance or susceptibility in the maize grain, grain screening would be the major option. Different researchers have used screening methods involving one or more resistance

parameters and succeeded in assessing maize resistance against weevil infestation. Widstrom et al. (1972) compared “grain weight loss, total number of weevil progenies that emerge, percentage of kernels damaged, percentage of parent mortality, percentage of progeny mortality”, and observed total progeny emergence as the most consistent and effective parameter for discriminating maize cultivars into different response classes. They further observed that grain weight loss would as well be used for estimating economic losses associated with weevil damage. Kim and Kossou (2003) successfully screened 164 maize cultivars basing on their variations in the frequency of oviposition by *S. zeamais*, the number of F₁ weevil progenies that emerged, proportion of damaged kernels, and the median development periods.

Various screening protocols have been developed and are being adopted for discriminating maize genotypes into different response classes (Dobie, 1974; Urrelo et al., 1990; Derera et al., 2010). Dobie (1974) used the median development period and total F₁ weevil progenies to develop a susceptibility index that discriminates maize genotypes into various response classes namely resistant, moderately resistant, moderately susceptible and susceptible based on their respective numeric values that usually ranges from 0 up to 13. This index is known as Dobie's index of susceptibility (DIS). However, Dobie's method is labour intensive and requires reasonable period of time to achieve good results. Urrelo et al. (1990) modified Dobie (1974) screening method by considering the number of eggs laid on the test cultivar and the days to first weevil emergence, instead of weevil progeny emergence and median development period, respectively, and reported that their method would save time. Gudrups et al., (2001) compared the two methods and indicated that the total time required by the Urrelo (1990) method was longer than that required for Dobie method. Furthermore, Gudrups et al. (2001) indicated that Urrelo et al. (1990) method would require shortening but without compromising its cultivar discrimination efficiency. On the other hand, Derera et al. (2010) developed a rapid and precise maize screening procedure that can save up to 40 days from the standard Dobie (1974).

Siwale et al. (2009) used grain hardness, grain weight loss, median development period, protein content, and DIS to assess resistance of 50 maize genotypes to weevil infestation. They observed significant differences in grain hardness and grain weight loss between resistant and susceptible genotypes. However, insignificant differences were observed among the 50 maize genotypes for protein content, and Dobie's indices of susceptibility in spite of the wide range of susceptibility index displayed; reasons for this shortfall may warrant further investigation.

Furthermore, Garcia-Lara et al. (2004) reported significant negative correlations between grain hardness and pericarp thickness to weevil susceptibility, and high proportions of phenolic acids and other compounds were detected in the pericarp, which they associated with grain hardness and hence a measure of weevil resistance. Therefore, simple, fast, low cost and precise maize screening methods would considerably save time and other resources required for effective screening of maize genotypes against weevil infestation.

1.9 Breeding for weevil resistance

Grain resistance against weevil infestation and damage is the most sustainable and cheapest method of minimizing weevil damage in maize especially at smallholder farmer level. Weevil resistance traits have been identified and improved in maize germplasm to enhance grain resistance against weevil damage (Tipping et al., 1989; Arnason et al., 1993; Dhliwayo and Pixley, 2003). Tipping et al. (1989) reported significant general combining ability effects towards the expression of weevil resistance in maize and further observed that environmental effects were influencing grain resistance against weevil infestation. Dhliwayo and Pixley (2003) improved 6 maize populations against weevil infestation through divergent selections among S_1 and S_2 lines. On the other hand, the occurrence of weevil resistance in both QPM and non-QPM maize hybrids reveals the possibility of introgressing weevil resistance in QPM germplasm (Arnason et al., 1993). However, inheritance of weevil resistance from parents to offsprings may be hindered by the limited correlation for weevil resistance between inbred line parents at their early stages of evaluation and their respective hybrids (Dari et al., 2010). This hindrance can be minimized by executing crosses between resistant by resistant parents to improve resistance in ensuing hybrids (Dhliwayo and Pixley, 2003). Similar results were reported by Widstrom et al. (1983) who observed that reciprocal crosses between weevil resistant parents were not significantly different from the main crosses.

Findings from Widstrom et al. (1983) and Dhliwayo and Pixley (2003) indicate that enhancement of weevil resistance in maize germplasm would require crossing resistant by resistant parents for maximum introgression of weevil resistance in the F_1 hybrids. Otherwise, crossing resistant by susceptible or vice versa, the resulting hybrids may not exhibit adequate levels of resistance because of the low correlation for weevil resistance between the inbred line parents and their hybrids (Dari et al., 2010). However, contrasting molecular genetics studies results reveals that even susceptible parents possess weevil resistance genes. García-Lara et al. (2009) reported

up to 50% of weevil resistance QTL alleles from the susceptible parent of 163 F_2 -population derived from a cross between weevil resistant and susceptible parents. These results portray the importance of additive gene action in the governance of weevil resistance.

1.10 Double fertilization and weevil resistance in maize

Double fertilization refers to two forms of fertilization; the first one is the fusion of one haploid male gamete with the oosphere to produce a diploid embryo, while the second fertilization is the fusion of another male gamete with the central cell to generate a triploid endosperm (Faure et al., 2003). The endosperm is the storage organ of the seed, thus it accumulates a number of nutrients including carbohydrates and proteins that are required by both human beings and insects. The triploid nature of the endosperm with $2n$ gametes derived from the seed parent and $1n$ gamete obtained from the pollen parent partly explains the manifestation of maternal effects towards weevil resistance. Consequently, differences in response to weevil infestations are exhibited in the hybrids, as a result of changes in the directions of the crosses between weevil resistant female parents and weevil susceptible male parents (Widstrom et al., 1983; Kang et al., 1995; Dari et al., 2010). For instance, if a weevil resistant genotype is used as a female (seed parent), and the susceptible one as a male parent, the resulting hybrid is likely to be weevil resistant because its endosperm will possess two doses of resistance and also the pericarp will be comprised of the resistant female tissue (Van Schoonhoven et al., 1975; Kang et al., 1995). However, Tipping et al. (1989) indicated that maternal effects may not be manifested beyond F_1 seed, which emphasizes the need to purchase new hybrid seed every season.

1.11 Generational effects on the manifestation of weevil resistance

Usually, the manifestation of seed-based traits such as weevil and ear rot resistance is influenced by the generation of the seed. This is because the maize seed possesses tissues of different generations. For example, crossing two parents generates F_1 hybrid seed, whose pericarp is constituted of only the maternal tissue of the female parent (Kang et al., 1995); the embryo and the endosperm, are generated as a result of fusion of the female and male gametes. Cultivation of F_1 seed leads to F_1 plants that produce F_2 seed. The pericarp tissue of the F_2 seed is basically the maternal tissue generated by the F_1 hybrid maize plants, whereas the embryo and the endosperm comprises of constituents from both the F_1 maternal gametes of

the seed parent and paternal gametes from the pollen parent (Faure et al., 2003). Thus, an extra seed-generation would be required for the new genotype of the hybrid to be expressed in the pericarp tissue (Van Schoonhoven et al., 1975). This implies that hybrid evaluation for weevil resistance would be more appropriate at F_2 seed generation when the genes from both parents are expected to be expressed in all tissues (embryo, endosperm and pericarp). However, evaluation of F_1 seed would be sufficient if high positive correlation for weevil resistance exists between F_1 and F_2 seed. This occurrence suggests the need for special consideration of the seed generation when evaluating maize germplasm for weevil resistance, and partly explains why there could be differences in grain response to weevil infestations between generations.

1.12 Maize improvement for weevil resistance through recurrent selection

Recurrent selection is a population improvement breeding method involving cyclic selection and crossing of individual genotypes with desired characteristics for generation of progenies which are advanced to subsequent selection cycles (Hallauer and Miranda, 1988). Duvick (1992) highlighted the significance of recurrent selection in enhancing genetic diversity in maize germplasm. Among the popular recurrent selection methods in maize breeding is the selfed progeny selection (S) with the advantage of direct selection which usually favours additive genetic effects as the masking effects are minimized (Hallauer and Miranda, 1988). Weyhrich et al. (1998) emphasized the value in executing selfed progeny recurrent selection (SPRS) as the rapid fixation of alleles as a result of exposure and ultimate elimination of deleterious genes in a particular population. Van Schoonhoven et al., (1975) reported increased maize weevil resistance in dent maize genotypes as a result of repeated selfing and selections. In the same regard this study explored the potential of single-selfing and two subsequent selections in enhancing maize weevil resistance, yield and foliar disease expression in Longe5, a popular maize population in Uganda.

1.13 Maize Foliar diseases

Foliar diseases constitute a major category of major constraints to maize production worldwide, with their economic importance and prevalence varying from one region to another. The incidence and severity of foliar diseases is influenced by the climatic conditions, especially temperature and relative humidity (Adipala et al., 1993) in addition to crop and residue

management practices (Bigirwa et al., 2001). Foliar diseases of economic significance in sub-Saharan Africa have been *Turcicum* leaf blight (*Exserohilum turcicum*), grey leaf spot (*Cercospora zeaе maydis*), maize streak virus disease, and rust (*Puccinia sorghi*) (Vivek et al., 2001). However, recent studies have indicated the increasing significance of *Phaeosphaeria* leaf spot (PLS) (Vivek et al., 2010).

Like in several other sub-Saharan countries, maize production in Uganda is seriously constrained by grey leaf spot, maize streak virus disease, and *Turcicum* leaf blight that are prevalent in all major maize growing regions (Adipala et al., 1993; Bigirwa et al., 2000; Bigirwa et al., 2003). The epidemiology, distribution, and severity of *Turcicum* leaf blight have been reported (Adipala et al., 1993). On the other hand, considerable work has been done towards understanding the epidemiology, prevalence, and characterization of the grey leaf spot isolates from Uganda, Kenya and Rwanda all geared at controlling the disease (Vivek et al., 2001; Asea et al., 2002; Okori et al., 2003). Nevertheless, in spite of the various research interventions, *Turcicum* leaf blight (TLB) and grey leaf spot (GLS) are still a major constraint to maize production in Uganda and eastern Africa sub region in general (Vivek et al., 2010).

In addition to TLB and GLS, common rust (*Puccinia sorghi*) is another important disease causing considerable yield losses in maize, more especially when it manifests in combination with other foliar diseases. In Uganda common rust is encountered in most maize growing areas but it is more prevalent in the high altitude areas especially the highland zones in Kapchorwa district; however, limited information is available regarding its economic importance. Integration of host plant resistance in the control of foliar diseases could offer a sustainable remedy to the major maize diseases (Pratt et al., 2003). Usually the maize crop is infected with a complex of more than one foliar disease and this may warrant enhancing resistance against multiple diseases. Therefore, pyramiding genes for foliar disease resistance would probably minimize yield loss associated with the complex of foliar disease infection. Vivek et al. (2010) reported significant positive correlations among a number of foliar diseases including GLS, TLB, MSV, common rust, head smut, ear rots and PLS. Thus the potential of pyramiding resistance genes for the most popular diseases needs to be explored. Molecular marker technology offers additional benefits in facilitating gene pyramiding (Asea et al., 2012). Information on the gene action governing the resistance of the major foliar diseases in the study germplasm would be a crucial step. Various germplasm may exhibit different gene action under different environments (Falconer, 1981), this may be a result of genotype by trait interactions.

1.14 Combining ability and gene action for maize traits

Combining ability studies provide information on the genetic worthiness or breeding value of a particular line for specific traits of interest. This information is important when identifying elite parents or parental combinations for a specific breeding strategy. The required information includes: general combining ability (GCA) which is the average performance of an inbred line in hybrid combination, in addition to specific combining ability (SCA), which refers to the deviation of the crosses on the basis of average performance of the lines involved in a cross. The significance of GCA for a particular trait is usually associated with the preponderance of additive gene action, whilst, the significance of SCA is usually associated with the governance of non-additive gene action, mainly manifested as dominant and/or epistatic gene effects, towards trait expression.

1.15 Combining ability and gene action under stress conditions

Numerous researchers have reported the significance of general and specific combining ability effects and associated gene action in the regulation of maize traits. Derera et al. (2007) reported the significance of GCA effects for grain yield and secondary traits under drought stress and a combination of GCA and SCA under drought free environments in southern Africa maize germplasm. These results reveal interactions between the genetic effects and the environment that may require considerations when designing evaluation trials. Another trial involving drought tolerance and *Striga* resistance was conducted on west and central African maize germplasm and significant GCA and SCA effects were observed for yield and secondary traits in Nigeria (Badu-Apraku et al., 2011). Regarding nitrogen- and drought-stresses, Makumbi et al., (2011) reported significant and predominant GCA effects for grain yield under water-stressed and well-watered environments, while SCA effects were significant under nitrogen-stress environments.

For maize diseases, Menkir and Ayodele (2005) reported significant GCA and SCA effects for grey leaf spot (GLS) resistance and secondary traits, in 96 hybrids generated from 24 mid-altitude inbred lines. Results from related studies indicated significant GCA effects for *Turcicum* leaf blight, grey leaf spot, rust, maize streak virus, head smuts, *Phaeosphaeria* leaf spot (PLS) and ear rots (Vivek et al., 2010). For downy mildew resistance on the other hand, Fato et al. (2012) reported significant GCA effects in tropical maize inbred lines and thus suggested the preponderance of additive gene action regulating its expression; while for yield they observed significant GCA and SCA effects.

Regarding combining ability for weevil resistance in maize, Kang et al. (1995) reported significant GCA, SCA and reciprocal effects from results of 90 single cross hybrids generated from a 10-parent full diallel crossing scheme. Kim and Kossou (2003) reported highly significant GCA and SCA effects from screening results of 144 experimental maize hybrids against the maize weevil. Dari et al. (2010) screened S_1 , S_2 , S_3 and S_4 populations and their respective single cross hybrids for weevil resistance and results from their genetic studies indicated significant GCA and SCA effects. On the other hand, García-Lara et al. (2009) reported varying gene actions to be responsible for different weevil resistance parameters in the maize grain. They reported grain damage, grain weight loss and Dobie index of susceptibility to be governed by dominant gene action; while antibiosis that maintains low numbers of weevil progenies was conditioned by additive gene action, in an F_2 maize population derived from “a weevil susceptible parent CML 290” and a “resistant parent Muneng-8128 co HC1-18-2-1-1”

Regarding the regulation of quality and maturity traits, Machida et al. (2010) reported significant GCA effects to be responsible for the governance of tryptophan, protein content, kernel endosperm modification, and anthesis dates. They further reported the significance of SCA effects for the governance of grain yield, while the reciprocal effects were important for the regulation of quality index, tryptophan and anthesis dates.

1.16 Mating designs used in estimation of combining ability

A number of mating designs are used to estimate combining ability effects in various crops. Some of the most popular mating designs used in maize genetics studies include diallel mating designs (Griffing, 1956). The Diallel mating designs have a major advantage of mating parents in all possible combinations, including the reciprocals for the full diallel mating scheme. Another group of mating designs involves bi-parental crosses, and is commonly known as the North Carolina designs I, II, and III (Comstock and Robinson, 1948). The line by tester mating design is another popular design in maize breeding.

1.17 Heterosis and crop improvement

Heterosis measures superiority in performance of a hybrid relative to its parents as regards to the specific trait(s) of interest. It is expressed as percentage gain in the manifestation of a trait in a hybrid over its parents. Usually heterosis portrays wide genetic divergence between the parents producing a hybrid (Hallauer and Miranda, 1988). Against this background, high

heterosis levels are expected from maize inbred lines of different heterotic groups. However, high heterosis levels can as well be exhibited between parents from the same heterotic group (Machida et al., 2010). This may be a result of complementarities within the heterotic group. More frequently, heterosis manifests the existence of dominance and epistatic effects (non-additive gene action) for the traits in which it is exhibited. Nevertheless, it gives the breeder the basis for measuring the degree of success in the improvement process of a particular study trait. Therefore, the higher it is, the better the hybrid ought to be as regards to the specific trait of interest.

Heterosis has been reported in a number of traits in various crops. In common beans, Mukankusi et al. (2011), reported considerable levels of heterosis, ranging from -10.0% to -42.2%, for *Fusarium* root rot resistance. In maize it has been reported by several researchers. Makumbi et al. (2011) reported high heterosis levels above 500% among single cross hybrids and their inbred line parents, under nitrogen and drought stress conditions. They associated the high levels with the poor performance of the usually unstable inbred line parents under stress, as opposed to the reasonable performance of their relatively stable single cross hybrids. Onwubiko and Onwubiko (2011) reported high levels of heterosis for grain yield and secondary traits, in addition to oil and lysine contents in 132 experimental maize hybrids. Fato et al. (2012) reported heterosis levels of up to 27% for grain yield in crosses between tropical maize inbred lines and populations ZM523 and Suwan-1.

1.18 Participatory plant breeding and selection of new maize cultivars

Participatory plant breeding (PPB) is a breeding strategy in which farmers and other key stakeholders are involved at some stages or all stages of germplasm selection, variety development and adoption (Witcombe et al., 2006). Farmer participation in the breeding process is vital because their key attributes desired in new crop varieties are timely identified and integrated in the new cultivar (Witcombe et al., 2006). Thus, PPB offers an opportunity for improving breeding efficiency by saving time and other resources because the right germplasm ought to be selected and utilized in the process. Bernardo (2003) highlights the significance of selecting the right parents for a specific trait of interest and indicates that use of inappropriate parents sacrifices genetic gain regardless of the superiority of the breeding method used.

The majority of farmers in Africa grow maize for both home consumption and income generation. Therefore, they grow various maize varieties mainly based on their taste and other quality related attributes but not necessarily yield (De Groote et al., 2010). Thus, farmer involvement especially at the early stages of trait identification and prioritization would be vital in the development and ultimate adoption of new crop varieties that suit their desires (Gyawali et al., 2006). Identification and integration of farmer preferred attributes and subsequent evaluation and selection of suitable parents is a vital step in the development of elite germplasm and ultimately new cultivars (Bernardo, 2003). Enormous benefits have been registered when farmers are involved in early germplasm evaluation and selection; for the costs are saved and adoption is enhanced as farmers only select genotypes that meet their satisfaction (Virk et al., 2003). A number of early maturing maize cultivars with superior yields were developed and readily adopted by farmers through PPB, which shortened the breeding period by at least two crop seasons, as compared to cultivar development by conventional methods (Witcombe et al., 2003). These results portray the significance of farmer participation in the breeding process, as it enhances timely needs assessments and provision of appropriate breeding solutions and therefore might need due consideration from breeders and other research partners.

1.19 Summary

From the literature reviewed, the importance of weevils in maize production is globally acknowledged, more especially in the tropical environments. The major control measure highlighted is the use of chemicals. However, their continued use has resulted in development of insecticide resistance by the weevils, in addition to the adverse toxic effects of chemicals to human beings animals and the environment. Germplasm with weevil resistance genes have been identified and used in a number of studies. However, limited weevil resistant cultivars seem to be accessed by farmers according to the literature available. There is also limited information on grain loss associated to weevil damage. This emphasizes the need to cover up these gaps, so as to minimize grain weight and/or quality loss during storage.

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Chapter Two

Farmers' perceptions about the maize weevil (*Sitophilus zeamais* Motschulsky) in maize and its control measures in Uganda

Abstract

The maize weevil (*Sitophilus zeamais* Motschulsky) is one of the most destructive pests affecting maize grain under storage. It is prevalent in most of the maize growing zones in the tropics and sub-tropics. A participatory rural appraisal was conducted in Kasese, Nakaseke and Kapchorwa districts from December 2010 to January 2011 to gather information on the maize weevil status in Uganda. The objectives of the study were: i) to assess farmers' knowledge on the weevil pest problem, its significance, and coping methods; and ii) to capture information on farmers' perceptions about improved maize varieties and the major attributes desired in new maize varieties. Personal interviews (semi-structured questionnaire), focus group discussions and transect walks were used to collect data from representative maize farmers. The socio-economic data were analyzed using STATA program; while prioritization of crop enterprises, maize variety attributes and production constraints was executed through matrix ranking. All respondents in Nakaseke and Kapchorwa districts and over 87% of respondents in Kasese district knew the maize weevil and its effects on maize. Over 53% of the respondents estimated grain weight loss associated with weevil infestations to reach 20% within a storage period of four months, while over 40% of the respondents estimated grain weight loss to be between 20 and 50% within the same storage period. Farmers were reportedly controlling weevils using wood ashes, red pepper and *Cupressus sempervirens* (Christmas tree), the efficacy of which ought to be established. The most highly ranked attributes desired in the new maize varieties included: high grain yield, tolerance to drought and low nitrogen stresses; resistance to foliar diseases, storage and field pests' resistance, in addition to early maturity. Therefore, development of high yielding, foliar disease and weevil resistant maize cultivars would greatly contribute towards sustainable maize productivity enhancement in the three study districts.

Keywords: maize weevil, storage, variety attributes, weevil damage, control measures.

2.1 Introduction

Maize (*Zea mays* L.) is the most important cereal crop in Uganda serving as food and cash crop, as well as a major ingredient for animal feeds. Maize is grown in all agro-ecological zones of Uganda ranging from the mid-altitude dry-zones of 800 – 1000 metres above sea level (m.a.s.l.) in Kasese district in western Uganda, through the mid-altitude wet-zones of 1001 – 1500 m.a.s.l. in Nakaseke, Mubende, Masindi, Iganga districts in central and eastern Uganda, up to the highland zones of 1501 to \geq 2200 m.a.s.l in Kapchorwa, Mbale and Sironko districts on the slopes of mountain Elgon in eastern Uganda. Throughout the growing zones, maize production is constrained by a number of factors including field pests such as stem borers and termites (Kalule et al., 1997); foliar diseases such as *Turcicum* leaf blight (*Exserohilum turcicum*), grey leaf spot (*Cercospora zeaе maydis*), rust (*Puccinia sorghi*) and maize streak virus (Bigirwa et al., 2003); ear and stalk rots (Bigirwa et al., 2007); and drought and nitrogen stresses (Bänziger and Diallo, 2001). Research has been conducted in response to some of these constraints. In addition to the field constraints, the maize grain is attacked by the maize weevil (*S. zeamais* Motsch.) during storage which causes significant losses in grain weight and quality throughout the maize growing zones of Uganda. Grain weight losses attributed to weevil infestation is not well-documented in Uganda. However, Ngatia and Kimondo (2011) reported grain weight loss of up to 20% in cribs and over 25% in houses, while comparing maize grain weight losses in two farmer environments under natural infestation in Kenya. In spite of the considerable losses in grain weight and value associated with the maize weevil, limited efforts have been made to curb the maize weevil problem in Uganda. Therefore, there is a great need to initiate collective efforts geared at controlling weevils at all critical points in the maize value chain and this warrants the involvement of farmers and other key players.

Participation of multiple stakeholders in problem identification and redress empowers them to be part of the research process, which improves output generation and evaluation, and ultimately enhances technology adoption. Accordingly, timely identification of the major attributes desired by farmers, guides research to incorporate these attributes in the new maize varieties, through selection of suitable parents that may generate superior varieties with the desired characteristics in a shorter period of time (Witcombe et al., 2003). In addition to shortening the breeding period, farmer participation in product development enhances technology adoption, and thus improves research efficiency and effectiveness (Witcombe et al., 1996). The superiority of new maize varieties is dependent on the effectiveness of the breeding

methodology involving careful selection of appropriate parents. Bernado et al. (2003) indicated that selection of inappropriate parents ought to limit genetic gain irrespective of the breeding method used. Thus, farmer participation is key towards careful evaluation and selection of suitable parents that are vital in the development of elite inbred lines and ultimately hybrids and synthetic populations.

Participatory rural appraisals (PRAs) offer an opportunity for researchers to interface with farmers and other key stakeholders to identify research needs and design appropriate research agenda. A PRA was conducted in three districts namely Kasese, Nakaseke and Kapchorwa that are representative of the major maize growing zones of Uganda, with the overall objective of studying farmers' perceptions of the maize weevil and its control measures in Uganda. The specific PRA objectives were: 1) to assess farmers' knowledge on the weevil pest problem, its significance in Uganda and farmer coping methods; 2) and to capture farmers' perceptions on improved maize varieties and the major attributes desired in new maize varieties.

2.2 Methodology

2.2.1 Study areas

The participatory rural appraisal (PRA) was conducted in Kasese, Nakaseke and Kapchorwa districts in December 2010 and January 2011. During this period the maize grain is about four to five months under storage, while the maize crop in the field is almost ready for harvesting, in Kasese and Nakaseke districts which experience two rainy seasons. In Kapchorwa district, where there is only one rainy season, during this period the maize grain is about two to three months under storage and they are beginning land preparations for subsequent planting in late February/early March. Kasese district is located in western Uganda, represented the mid-altitude dry zones of Uganda, with altitude ranging from ≤ 800 to 1000 m.a.s.l., Nakaseke district in central Uganda represented the mid-altitude wet zones, with altitude between 1001 and 1500 m.a.s.l, and Kapchorwa district in eastern Uganda represented the highland zones with altitude between 1501 to ≤ 2200 m.a.s.l (Figure 2.1). Three sub-counties were covered in Kasese and Nakaseke districts each, while four sub-counties were covered in Kapchorwa district.

2.2.2 PRA tools

The PRA tools used were personal interviews at household level, focus group discussions and transect walks.



Figure 2.1: Map of Uganda showing the study districts (in red).

Source: www.nationsonline.org/oneworld/map/Uganda-map.htm

2.2.2.1 Personal interviews

Personal interviews were conducted at household level with the aid of a semi-structured questionnaire. Respondents were randomly (each farmer was assigned a random number) selected from the list of maize farmers provided by the sub-county extension officer at each of the participating sub-counties. With the guidance of the sub-county extension officers selected farmers were accessed, introduced, and interviewed. For Kasese and Kapchorwa districts where there were communication barriers due to language differences, the extension officers in the respective sub-counties served as translators. A total of 100 maize farmers were interviewed; 33 in Kasese and Nakaseke districts each and 34 in Kapchorwa district.

Aspects on which data were recorded included: size of farm land, this was estimated in relation to one hectare (100 m x 100 m), the major crops grown and the respective areas cultivated for each crop. Other aspects on which data were collected included: the importance of maize as one of the farm enterprises, maize yields, purposes for which maize is grown; major maize varieties grown and the source of seed, the main characteristics of the varieties grown and the major attributes that would be desired in new maize varieties. Furthermore, data were collected on the major constraints affecting maize production, the coping methods, and knowledge of, and significance of the maize weevil in maize production and storage. Maize yield was estimated as the number of 100 kg-bags obtained from one ha and later converted to $t\ ha^{-1}$. On the other hand, grain weight loss was estimated as the average reduction in grain quantity (kg) after an average storage period of four months (about 122 days), for which most of the farmers store their maize grain, before a new crop sets in. During the exercise, maize samples were collected from volunteer-farmers, for subsequent incubation and assessment for weevil infestation and damage in the maize screening laboratory at the National Crops Resources Research Institute (NaCRRI), Namulonge. At least 20 samples of average weight 0.5 kg each were collected from each sub-county.

2.2.2.2 Focus group discussions

To substantiate the information obtained from personal interviews, focus group discussions were also conducted at sub-county level, with one focus group discussion per sub-county (Figure 2.2). Farmer mobilization was done by sub-county extension officers together with lead

farmers, 10 – 20 farmers participated per sub-county. During farmer mobilization, gender composition was a key criterion; accordingly it was ensured that at least 40% of the participating farmers were females. All focus group discussions were convened at the sub-county headquarters. Participating farmers were first briefed about the broader perspective of the study with regards to income generating activities in general and agricultural production in particular. Later on the specific aspects of maize and other crops' production and productivity, such as acreage, yield, importance, access to agro-inputs, production constraints, storage and produce prices were highlighted. In the course of the discussions, at least five nearby farmers per sub-county who still had maize, in addition to other crops in the field, were asked to lead the group to their crop fields for purposes of capturing more information on the farming characteristics of the study community.



Figure 2. 2: A focus group discussion in Nakaseke district

2.2.2.3 Transect walks

Transect walks covering two to three fields were conducted per sub-county. From the transect walks more information was obtained on the farming system in general and maize production characteristics in particular. Transect walks were also used to ascertain some of the information obtained from personal interviews and focus group discussions. Aspects considered during the exercise included: average farm land area, the main crops grown, the proportion of land covered by maize as compared to the entire farm land, and the prevailing production constraints

encountered. At least five additional maize grain samples of about 0.5 kg were collected from each sub-county from farmers who participated in the transect walks. Farmers from whom grain samples were collected were randomly selected from the list of participating farmers. A total of 78 maize grain samples were collected for this purpose.

2.2.3 Assessing maize importance and its production constraints

Such data were captured from focus group discussions. Matrix ranking was done to determine the relative importance of maize as compared to other crops, i.e. prioritization of maize among other crop enterprises, the average area under maize production, constraints hindering maize production, and the various attributes desired in maize varieties. To determine the relative importance of the major crops grown, eight major crops were listed in each of the three study districts. Ranks of 1 (as the most important), through 2, 3, and 4, with moderately varying importance, up to 5 as the least important, were used for crop prioritization. The five ranks of 1, 2, 3, 4 and 5 were each multiplied with weights of 5, 4, 3, 2 and 1, respectively, in order to get the overall rank for each crop per district.

2.2.4 Assessing maize grain samples for weevil infestation and damage

The grain samples collected from the study areas were assessed for weevil infestation and damage in the laboratory at the National Crops Resources Research Institute (NaCRRI), Namulonge. Eight replications of 50 g each were sieved and put in 250 cm³ glass jars with perforated lids fitted with wire meshes of pore size less than 1.0 mm, to allow free ventilation while stopping weevils from escaping out of the jars. The glass jars with maize grain samples were laid out in the laboratory room as a randomized complete block design (with 8 replications). The samples were incubated in the laboratory at a temperature of 28±2°C and a relative humidity of 70±5%, which are optimal conditions for weevil growth and multiplication (Tefera et al., 2010). The samples were left uninterrupted under these laboratory conditions for three months, after which weevil counts were recorded per sample and the new sample weights determined. Percent weight loss was calculated as follows:

$$\text{Weight loss (\%)} = \frac{\text{Original sample weight} - \text{new sample weight}}{\text{Original sample weight}} \times 100$$

2.2.5 Data analysis

The socio-economic data on family demography, farm size, major crop enterprises engaged in and the scale of operation were subjected to STATA for analysis, while the biological data on weevil infestation and damage was subjected to GenStat 14th edition (Payne et al., 2011).

2.3 Results

2.3.1 Demographic distribution of respondents

In Kasese district 45% of the respondents were women, in Nakaseke district 26% of the respondents were women, while in Kapchorwa district 39% of the respondents were women. For household headship, 28% of the households interviewed in Kasese district were headed by women, 19% of the households interviewed in Nakaseke were headed by women, while in Kapchorwa district 3% of the households interviewed were headed by women.

2.3.2 Size of farm land

The size of land used for agricultural production and the percentage of farmers owning the varying sizes in Kasese, Nakaseke and Kapchorwa districts is shown in Table 2.1. The overall availability of land for agricultural production in the three districts was distributed as follows: 87.9% of the respondents had 0.3 to 5.0 ha, 7.7% had 5.0 to 10.0 ha, while the remaining 4.4% had more than 10.0 ha.

Table 2.1: Land size and percentage of farmers owning it in Kasese, Nakaseke and Kapchorwa districts

District	Farm size (ha)	Proportion of farmers (%)
Kasese	0.25 – 5.00	95.00
	5.01 – 10.00	5.00
	>10.00	0.00
Nakaseke	0.25 – 5.00	77.40
	5.01 – 10.00	16.10
	>10.00	6.50
Kapchorwa	0.25 – 5.00	96.80
	5.01 – 10.00	3.20
	>10.00	0.00

2.3.3 Main crops grown

The main crops grown in each of the three districts are given in Table 2.2. The results indicated that maize, beans, cassava, *Solanum* potato, sweet potato, bananas, groundnuts and tomatoes were the major crops grown in Kasese district, in their order of importance. In Nakaseke district it was bananas, maize, beans, cassava, sweet potatoes, coffee, groundnuts and tomatoes, also ranked in their order of importance; while in Kapchorwa district, it was maize, bananas, wheat, beans, coffee, *Solanum* potatoes, barley and tomatoes as their major crops, ranked in their order of importance.

2.3.4 Area of land for maize production

In Kasese district, 97.0% of the respondents were using up to 50.0% of their land for maize production, while 3.0% (especially those with farm land of size 6.0 to 10.0 ha) were allocating more than 50.0% of their land to maize production. For Nakaseke district, all respondents (100.0%) were allocating up to 50.0% of their land to maize production. For Kapchorwa district on the other hand, 94.0% of the respondents were allocating up to 50.0% of their land to maize

production, while the remaining 6.0% of the respondents were allocating over 50.0% of their land to maize production.

Table 2.2: List of the eight major crops grown in Kasese, Nakaseke and Kapchorwa districts

District	Crop	Rank 1 (x 5)	Rank 2 (x 4)	Rank 3 (x 3)	Rank 4 (x 2)	Rank 5 (x 1)	Composite score	Overall rank
Kasese	Maize	17	14	8	0	0	165	1
	Beans	10	10	9	6	4	133	2
	Cassava	4	12	14	7	2	126	3
	Solanum potato	0	7	21	9	2	111	4
	Sweetpotato	3	2	18	15	1	108	5
	Bananas	0	0	21	12	6	93	6
	Groundnuts	0	0	3	31	5	76	7
	Sorghum	2	2	1	16	18	71	8
Nakaseke	Bananas	15	13	11	0	0	160	1
	Maize	9	8	18	4	0	139	2
	Beans	2	6	19	9	3	112	3
	Cassava	4	5	17	7	6	111	4
	Sweet potatoes	3	3	23	4	6	110	5
	Coffee	0	3	13	19	4	93	6
	Groundnuts	0	1	1	30	7	74	7
	Tomatoes	0	1	2	24	12	70	8
Kapchorwa	Maize	18	17	5	2	0	177	1
	Banana	7	14	17	1	3	147	2
	Wheat	3	4	15	16	4	112	3
	Beans	0	6	9	22	5	100	4
	Coffee	5	5	4	13	15	98	5
	Solanum potato	0	3	15	14	10	95	6
	Barley	0	1	3	32	6	83	7
	Tomatoes	0	0	2	33	7	79	8

2.3.5 Frequency of maize production

Maize was the main crop regularly grown in the three study districts. In Kasese district 61.7% of the respondents were growing maize every season, that is twice a year, while 38.3% were growing it once a year. For Nakaseke district, 87.1% of the respondents were growing maize twice a year (every season), while 12.9% were growing it once a year. For Kapchorwa district

on the other hand, 83.9% of the respondents were growing maize once a year, while 16.1% of the respondents were growing maize twice a year.

2.3.6 Common maize varieties grown

Results of the major maize varieties commonly grown in Kasese, Nakaseke and Kapchorwa districts are presented in Table 2.3. The popularity of the different maize varieties varied from one district to another. The results were considering each of the varieties presented in Table 2.3 as the major variety relative to the rest of the varieties grown by each of the respondents. Accordingly, in Kasese district, 31.0% of the respondents were reportedly growing Longe5¹, 24.0% were growing Longe6H, 15% were growing DK831, 12.0% were growing Longe4, while Longe1 and the local landraces were each being grown by 9.0% of the respondents, as the major variety for each. In Nakaseke district 40.0% of the respondents were reportedly growing Longe5, 24.0% were growing Longe4, 18.0% were growing Longe6H, 12.0% were growing the local landraces whereas 6.0% were growing Longe1. For Kapchorwa district on the other hand, the most popular variety was H614D² that was reportedly grown by 62.0% of the respondents. The remaining 38.0% of the respondents, especially in the transition zones of altitude ranging from 1501 to 1700 m.a.s.l., were reportedly growing both H614D and DK831.

Table 2.3: The major maize varieties grown in each of the three study districts

Farmers growing each variety as a major crop per district					
Variety	Type	Kasese	Nakaseke	Kapchorwa	Total
Longe1	OPV	3	2	0	5
Longe4	OPV	4	8	0	12
Longe5	OPV	10	13	0	23
Longe6H	Hybrid	8	6	0	14
Landraces	Landrace	3	4	0	7
H614D	Hybrid	0	0	21	21
DK831	Hybrid	5	0	13	18
Total		33	33	34	100

¹ Longe5 is a quality protein open pollinated maize variety released by the National Agricultural Research Organisation (NARO) in 1998, it is one of the most popular varieties adapted to the mid altitude zones of Uganda. Other open pollinated varieties include: Longe1 and Longe4; while hybrids include: Longe6H, Longe7H, Longe9H, Longe10H, Longe11H, and DK831 among others.

² H614D is a hybrid maize cultivar adapted to the highland zones of Uganda, its being marketed by Kenya Seed Company.

2.3.7 Sources of seed and average maize yields

Results from Kasese district indicated that, 25.0% of the farmers were purchasing maize seed from their local farm supply shops, 10.0% of the farmers were reportedly obtaining maize seed from their local sub-counties under the National Agricultural Advisory Services (NAADS) program, 47.0% of the farmers were purchasing maize seed from the local grocery shops, while 18.0% were recycling their seed from one season to another. In Nakaseke district, 30.0% of the respondents were purchasing seed from agro-input shops, 25.0% were obtaining free seed from the Sub-county National Agricultural Advisory Services (NAADS) program and non-governmental organizations operating in their locality, while 45.0% were recycling seed from previous seasons. For Kapchorwa district, 70% of the respondents were purchasing seed from agro-input shops, 10.0% were buying it from local groceries, while 20.0% were recycling it for at most three seasons.

Regarding average grain yield, results from the three districts are presented in Table 2.4. The results were recorded for maize grown as a mono crop. For Kasese district, 18.2% of the farmers were producing between 1.0 and 2.0 t ha⁻¹, 48.5% of farmers were producing between 2.0 and 3.0 t ha⁻¹, 27.3% of farmers were producing between 3.0 and 4.0 t ha⁻¹, while 6.0% were producing between 4.0 and 5.0 t ha⁻¹. For Nakaseke district, 87.9% of the maize farmers were producing an average yield between 1.0 and 2.0 t ha⁻¹, while 12.1% were producing between 2.0 and 3.0 t ha⁻¹. In Kapchorwa district, 38.2% of the maize farmers were producing average maize yields between 1.0 and 2.0 t ha⁻¹, 47.1% of farmers were producing between 2.0 and 3.0 t ha⁻¹, 11.8% were producing between 3.0 and 4.0 t ha⁻¹, while 3.0% were producing between 4.0 and 5.0 t ha⁻¹.

Table 2.4: The average yields when maize is grown as a mono crop in each of the three districts

Yield (t ha ⁻¹)	Number of respondents per district			
	Kasese	Nakaseke	Kapchorwa	Total (%)
1.00 – 1.50	2	20	5	27.00
1.51 – 2.00	4	9	8	21.00
2.01 – 2.50	9	2	5	16.00
2.51 – 3.00	7	2	11	20.00
3.01 – 3.50	4	0	1	5.00
3.51 – 4.00	5	0	3	8.00
4.01 – 4.50	2	0	0	2.00
4.51 – 5.00	0	0	1	1.00
Total	33	33	34	100.00

2.3.8 Maize production constraints in Kasese, Nakaseke and Kapchorwa districts

The constraints encountered during maize production are presented in table 2.5. The major production constraints varied from one district to another. In Kasese district, the maize production constraints were high input prices, low grain prices, maize weevil/poor storage, labour shortage, stemborers, unreliable rainfall, termites, diseases, soil exhaustion, and vermin (monkeys, rats and squirrels), in their order of importance. In Nakaseke district, the production constraints were high input prices, stemborers, maize weevil/poor storage, labour shortage, soil exhaustion, limited access to seed, low grain prices, diseases, drought, and vermin; while for Kapchorwa district they were labour shortage, high input prices, stemborers, soil erosion, grain damage by maize weevil, low grain prices, diseases, limited access to seed, unreliable rainfall and soil exhaustion.

Table 2.5: The major production constraints most encountered during maize production

District	Crop	Rank 1 (x 5)	Rank 2 (x 4)	Rank 3 (x 3)	Rank 4 (x 2)	Rank 5 (x 1)	Composite score	Overall score
Kasese	High input prices	2	19	11	6	1	132	1
	Stemborers	4	5	17	10	3	114	2
	Maize weevil	2	5	21	6	5	110	3
	Labour shortage	3	10	8	9	9	106	4
	Soil exhaustion	3	7	11	7	11	101	5
	Poor seed	3	8	2	12	14	91	6
	Low grain prices	3	1	10	4	21	78	7
	Diseases	0	2	8	6	23	67	8
	Drought	0	2	3	11	23	62	9
	Vermin	0	0	3	3	33	48	10
Nakaseke	High input prices	7	10	13	3	6	126	1
	Low grain prices	5	12	10	5	7	120	2
	Maize weevil	4	3	18	12	2	112	3
	Labour shortage	2	5	15	8	9	100	4
	Stemborers	2	3	2	24	8	84	5
	Unreliable rainfall	1	2	10	9	17	78	6
	Termites	2	2	4	2	29	63	7
	Diseases	1	2	1	8	27	59	8
	Soil exhaustion	3	0	1	1	34	54	9
	Vermin	0	1	1	2	35	46	10
Kapchorwa	Labour shortage	11	6	8	13	4	133	1
	High input prices	3	5	25	4	5	123	2
	Stemborers	5	7	8	15	7	114	3
	Soil erosion	3	2	3	24	10	90	4
	Maize weevil	1	4	3	19	15	83	5
	Low grain prices	3	2	5	3	29	73	6
	Diseases	0	3	4	7	28	66	7
	Poor seed	1	3	0	3	35	58	8
	Unreliable rainfall	1	2	0	1	38	53	9
	Soil exhaustion	2	0	0	1	38	50	10

2.3.9 The major attributes desired in a new maize variety

The attributes desired in new maize varieties were cutting across the three districts. The list of traits ranked included: grain yield, disease resistance, drought tolerance, tolerance to low nitrogen, resistance to field pests, and good storability/resistance to the maize weevil. Yield was

ranked as the most important trait desired in a new maize variety by 32.4% of farmers; this was followed by field pest resistance which was ranked second by 22.6% of farmers; good storability/resistance to the maize weevil was ranked third by 18.2 farmers; drought tolerance was ranked fourth by 14.3% of farmers; disease resistance was ranked fifth by 6.4% of farmers, while tolerance to low nitrogen was ranked sixth with 6.1%.

2.3.10 Farmers' knowledge on the maize weevil and coping methods

Most farmers in the study districts had knowledge on the maize weevil and had coping methods in place. For instance 100.0% of farmers interviewed in Kapchorwa knew the maize weevil, how it can be controlled and other crops that may be attacked by the maize weevil. Similarly, 100.0% of farmers in Nakaseke had knowledge on weevils and their control, while in Kasese district 81.8% of farmers were knowledgeable about the maize weevil and its control measures. The maize weevil control measures, as revealed by respondents from the three study districts included: proper grain drying before storage, followed by periodic drying; addition of ash and red pepper to the grain under storage; use of botanicals like *Cupressus sempervirens* (Christmas tree), under storage; dusting with insecticides especially malathion; delayed harvesting until a low moisture content is attained; for big farmers proper storage facilities (maize cribs and stores) were used, for which proper sanitation was observed together with regular fumigation (with Zinc or Aluminium phosphide), to ensure that the weevil's development cycle is broken.

2.3.11 Storage period before grain is sold

Grain infestation by the maize weevil usually begins in the field and on harvesting they continue multiplying until their damage symptoms manifest. Therefore, the storage period and the type of storage facility determine the extent of damage weevils' cause to the grain during storage. The survey results revealed that the storage period for the maize grain varied from district to district depending on the season and the prevailing market price for the grain. For instance, in Kapchorwa district where there is only one long rainy season spreading from March to October every year, harvesting usually begins in October and the grain can be stored up to the month of May the following year when a reasonable market value has been attained. Accordingly, 51.6% of the respondents in Kapchorwa district indicated that they sell their grain within three months after harvesting, 41.9% said they sell their grain within 6 months after harvesting, while 6.5% sold their grain beyond 6 months after harvesting. Results from Kasese district indicated that all

respondents (100.0%) sold their grain within three months after harvesting and only retained a few kilograms for their home consumption. For Nakaseke district, 83.9% of the farmers sold their grain within three months of harvesting, while the remaining 16.1% sold it between three and six months after harvesting.

2.3.12 Storage facilities

Storage remains a big challenge in maize production as different farmers use different means of storage depending on the region. For a number of maize growing areas, the maize crib was the most popular structure used for grain storage. A modern maize crib is shown in Figure 2.3a, while a traditional maize crib (granary) is shown in Figure 2.3b. PRA results revealed that the commonest structure used for storing maize in the study districts was the maize crib which was used by 90.3% and 69.0% of farmers in Kapchorwa and Kasese districts, respectively. For Nakaseke district 19.4% of farmers were using the maize crib. Other storage methods reported included small rooms in the main houses designated for storing farm produce, small stores constructed near the main houses, and gunny bags for storing shelled maize (grains) ready for sale.



a **b**
Figure 2. 3: Some of the most common storage facilities. a: a modern maize crib, b: a traditional maize crib (granary)

2.3.13 Estimated weight loss associated with weevil infestation

As regards grain weight loss associated with weevil infestation in four months of storage, 53.8% of the combined responses from the three districts indicated a weight loss of up to 20.0%, while the remaining 46.2% indicated a weight loss of 21.0 – 50.0%. At individual district level a similar trend was reported in Kasese and Kapchorwa districts with 58.6% and 61.3% of respondents reporting weight losses of up to 20% in four months of storage, and 41.4% and 38.7% reporting weight losses of 21.0 – 50.0% in Kasese and Kapchorwa districts, respectively. For Nakaseke district, 41.9% of the respondents reported weight losses between 0.0 and 20.0%, while 58.1% reported weight losses between 21.0 and 50.0%.

Regarding differences in variety response to weevil infestation, 35.0% of the respondents reported differences in maize varietal response to weevil infestation, with some varieties especially the small seeded flint varieties, taking longer to be infested and on infestation they exhibited less damage, compared to the dent large seeded varieties. The remaining respondents (65.0%) had not taken keen interest in this attribute.

2.3.14 Infestation and damage levels in the sampled maize grains

Results obtained from the incubated samples collected during the PRA revealed significant differences in percent infestation, number of weevils per sample, grain damage and weight loss. For sample infestation with the maize weevil, 59.0% of the maize grain samples collected from Kapchorwa district were infested, 41.0% were weevil free. For Kasese district, 96.0% of the grain samples were infested with the maize weevil, while only 4.0% were not infested. For Nakaseke district on the other hand, 87.0% of the grain samples were weevil infested and 13.0% were not infested. Regarding the number of weevils per sample Kapchorwa district had the least mean number of weevils per sample (43.3 weevils), which was significantly ($P < 0.001$) lower than Nakaseke (100.4) and Kasese (105.4) districts (Figure 2.2). The mean number of weevils in grain samples from Kasese district was not significantly ($P > 0.05$) different from that obtained in samples from Nakaseke district. Results of grain damage and weight loss followed the same trend, as the two parameters are dependent on the number of weevils per sample.

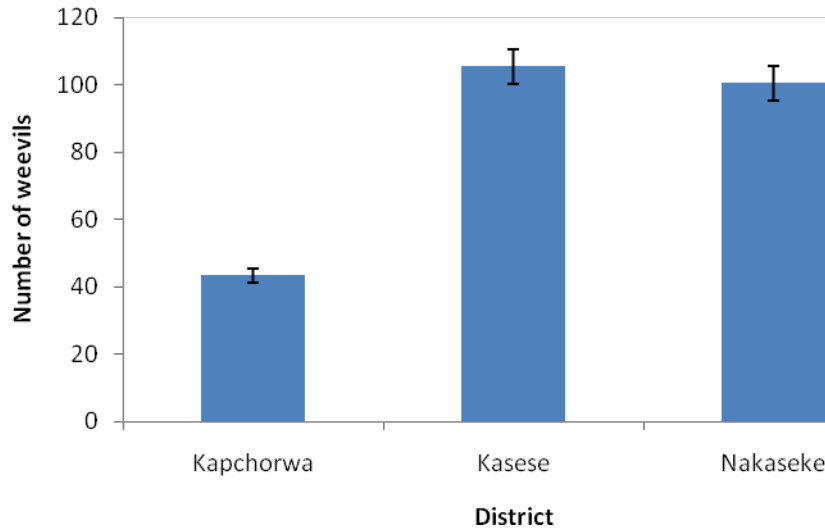


Figure 2. 4: Histogram of mean number of maize weevils recorded in maize grain samples obtained from Kapchorwa, Kasese and Nakaseke districts

2.4 Discussion

2.4.1 Demographic distribution of respondents

Results on the demographic distribution of respondents revealed that a reasonable proportion of female respondents (over 36.0%), participated in personal interviews and more than 40.0% of the participants in the focus group discussions were female. Therefore, the information given in this report took into account gender issues that would be related to maize production in the three study districts.

2.4.2 Major crop varieties grown

Results of the major crops grown in Kasese, Nakaseke and Kapchorwa districts revealed that farmers were growing various crops including: bananas (Matooke), maize, *Solanum* potatoes, sweet potatoes, beans, cassava, coffee, groundnut, and tomatoes, for both food and income generation. In all districts maize featured prominently among the most important crops. For instance, in Kasese and Kapchorwa districts maize was the most important crop, while in Nakaseke district it was the second important crop. The significance of maize in these districts justifies interventions towards enhancing its productivity. However, considering the size of land used for maize cultivation (it ranged from 0.3 to 5.0 ha for most of the respondents) and farmers'

involvement in the production of several other crops implied that maize production is mainly at smallholder scale. Therefore, interventions aimed at improving maize productivity and farmers' livelihood in general would require targeting smallholder farmers. Strategies targeting group dynamics such as capacity building, improved access to agro-inputs, and produce marketing would all be appropriate for such categories of farmers. Nevertheless, for the small proportion of farmers operating above 10.0 ha, other interventions may be more appropriate.

2.4.3 Frequency of maize production

Results of the frequency of maize production indicated that the majority (over 60.0%) of farmers in Kasese and Nakaseke districts were growing maize twice a year, while over 80.0% of farmers in Kapchorwa were growing maize one a year. The differences in the rainfall patterns (seasonality) of the three districts could be partly responsible for the frequency of maize production. In Nakaseke and Kasese districts which enjoy two rainy seasons per year, the majority of farmers were able to plant maize in the two rainy seasons. The few farmers who were planting once in a year were mainly limited by land, labour and other production constraints. On the other hand, the majority of farmers in Kapchorwa district were growing maize once a year mainly because the vast parts of the district that lie above altitudes between 1701 and 2200 m.a.s.l, mainly receive one long rainy season per year that stretches from March to September every year.

Additionally, because of the cold temperatures, the maize crop takes a longer period to mature (over six months) and thus two maize crop cycles are not possible per year. It is only in the transition zone in lower Kapchorwa with altitudes ranging from 1501 to 1700 m.a.s.l. where maize was grown twice a year. It is in the same area where most of the farmers constituting the 16.1% of the respondents that were growing maize twice a year were residing. Cultivation of maize once a year may, however, have beneficial effects towards breaking pests and diseases cycles and this ought to reduce pest and disease buildup. For Kasese and Nakaseke districts where the majority of farmers were planting maize on the same pieces of land twice a year, there were fewer chances of resting the land, nor rotating with other crops. This practice puts maize and other crops grown in such areas at a risk of pest and disease build up since there were limited chances of breaking their cycles. This occurrence partly explained why there were higher maize weevil prevalence in Kasese and Nakaseke districts, where the majority of farmers stored part of their maize produce (for home consumption) throughout the year. The remnant

maize stock serves as source of weevil infestations to the new maize grain stock (Giles and Ashman, 1971). For the vast parts of Kapchorwa district where they only grew maize once a year, their stores were cleared for certain periods of the year and this minimized remnant grain that would serve as source of weevil infestation for new grain stock.

Furthermore, the low mean minimum monthly temperatures, experienced in Kapchorwa district that usually go below 14°C might have been responsible for the lower maize weevil prevalence. Barney et al. (1991) and Ileleji et al. (2007) observed minimal weevil activities at temperatures below 15°C and above 36°C. On the other hand, the higher maize weevil prevalence in Kasese and Nakaseke districts could be explained by the favourable mean minimum and maximum monthly temperatures experienced in the two districts that usually range between 16 and 34°C, which are within the range of maximum weevil activity (Barney et al., 1991).

2.4.4 Seed sources and average yields

The seed is the plant organ with the highest yield potential for any crop; therefore, seed quality is a key component of sustainable maize production and productivity. Hence a need to obtain seed from reliable sources for which quality is guaranteed. The PRA results indicated that only 25.0% of farmers in the three districts were able to buy seed regularly from farm supply shops, 10.0% were relying on government “seed handouts”, 47.0% were buying seed from unreliable sources (general groceries), while 18.0% were recycling seed from one season to another. These results portrayed farmers’ limited access to improved seed, which was also reflected in the ensuing yields, whereby close to 50.0% of the farmers were obtaining yields between 1.0 and 2.0 t ha⁻¹. The results suggested the need for more farmer sensitization about quality seed and its sources, in addition to enhancing quality seed availability, for example, through farmer group seed purchase.

2.4.5 Farmers’ knowledge about the maize weevil

All farmers in Nakaseke and Kapchorwa districts were aware of the maize weevil and its control measures, while 81.0% of the farmers in Kasese district were aware of the maize and its control strategies, the remaining 19.0% of farmers in Kasese district were not aware of weevil control measures. Knowledge of the maize weevil and its control measures was a manifestation of the significance of the maize weevil in maize production and storage. Therefore, some of the control measures highlighted such as the use of red paper, *Cupressus sempervirens* and wood ash

would require validation as indigenous technical knowledge (ITK), for enhancing their potential towards complementing host plant resistance (Demissie, et al 2008). Among the common maize weevil control strategies mentioned by farmers was proper grain drying and storage. Grain storage is another important aspect affecting grain quality through regulation of grain moisture content, moisture content below 13.0% is reported to minimize weevil activity and ultimately reduces grain damage (Tefera et al. 2011).

The most popular storage facility reported in Kasese and Kapchorwa districts was the maize crib, usually constructed from locally available construction materials (mainly reeds, poles from local shrubs and grass for thatching). Grain storage was a big challenge mainly in Nakaseke and to some extent Kasese district and this could be one of the main reasons why farmers were selling most of their grain shortly after harvest. Grain sale immediately after harvesting is reportedly one of the practices reducing maize profitability as prices tend to drop significantly due to the abundance of maize grain on the market during this period of the year (Kimenju 2009). Therefore, more efforts would be required to sensitize farmers about grain storage and quality assurance during storage; regulation of weevil activity to minimal levels under storage ought to be emphasized. Grain resistance against the maize weevil would be the most sustainable way of ensuring grain quality under storage (Tefera et al. 2011).

The common maize varieties grown in Kasese and Nakaseke districts were Longe1, Longe4, Longe5, Longe6H³ and local landraces; Longe5 was the most popular variety grown in the two districts followed by Longe6H. The local landraces were also still popular in the study areas as they were reportedly being grown by 11.0% of the respondents; however, on further probing, it was found out that some of the cultivars described as local landraces were actually recycled grain of improved open pollinated varieties, especially Longe4 and Longe5. For Kapchorwa district, the most popular variety grown was H614D, which is a highland adapted maize hybrid imported from Kenya, and hence its availability on the market was not very consistent. The second popular variety reportedly grown in Kapchorwa was DK831, which is a hybrid, adapted to mid-altitude zones. Therefore, it would be necessary to verify whether it was DK831 that is as well adaptable to highland environments, or to establish the identity of that variety grown as DK831.

³ Longe6H is a three way cross maize hybrid, released by the National Agricultural Research Organisation (NARO). All Longe varieties designated by the suffix "H" signify hybrids, while those without it are open pollinated varieties (OPV), e.g. Longe5.

For Kasese and Nakaseke districts, the popularity of the old Longe varieties (Longe1, Longe4, Longe5 and Longe6H), other than the new Longe varieties (Longe9H, Longe10H, and Longe11H), suggested the need for enhancing the popularity of the new hybrids with superior attributes such as high yields and drought tolerance in the short run. The long term intervention would be development of new maize varieties with farmer desired attributes that include: high grain yield, weevil resistance, tolerance to drought and low nitrogen stresses, pest and disease resistance. On the other hand, the absence of locally developed maize cultivars adaptable to the highland ecologies in Kapchorwa and other districts in the highland zones would justify boosting the highland breeding program, while prioritizing grain yield, agronomic characteristics and weevil resistance as one of the key attributes during germplasm enhancement.

2.5 Conclusion

The PRA results indicated that the maize weevil was an important pest of maize in Kasese, Nakaseke and Kapchorwa districts causing significant grain weight losses that may exceed 20.0% within a storage period of four months. Farmers were reportedly controlling weevils using wood ashes, red pepper and *Cupressus sempervirens*, the efficacy of which ought to be established. Development of high yielding weevil and foliar disease resistant maize cultivars with tolerance to drought and low nitrogen stresses would contribute towards sustainable enhancement of maize productivity, storability and ultimately profitability in the three districts and Uganda in general.

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Chapter Three

Determining the genotypic variation for maize weevil and foliar diseases resistance in eastern and southern Africa maize germplasm lines

Abstract

The maize weevil (*Sitophilus zeamais* Motschulsky) is the most destructive storage insect pest of maize (*Zea mays* L.) in tropical Africa and worldwide, especially when susceptible varieties are grown. Grain resistance against weevils should be part of a major component of an integrated weevil management strategy. A total of 180 inbred lines from three different geographical areas were screened for maize weevil and foliar disease resistance. Screening was executed by infesting 32 newly emerged adult weevils into maize grain of 50 g, placed in 250 cm³ glass jars in a “no-choice” laboratory test. The experiment was laid out in the laboratory in a randomized complete block design, with three replications. The grain susceptibility parameters used were F₁ weevil progeny emergence, percent grain damage, median development period, Dobie’s index of susceptibility, and parental weevil mortality. New sources of weevil resistance for maize breeding were identified. Eight inbred lines (MV21, MV23, MV75, MV102, MV142, MV154, MV157, and MV170) were consistently grouped in the resistant class, and therefore selected as potential donors for weevil resistance in the maize improvement programs. There was significant and large genetic variation, and high levels of heritability (89 – 96%) for weevil resistance that suggested the high potential for germplasm improvement through selection. Results revealed that there was no significant association between maize weevil resistance and grain yield. Therefore, breeding for maize weevil resistance can be achieved without compromising grain yield.

Key words: Grain yield, maize, maize weevil, screening, weevil resistance.

3.1 Introduction

The maize weevil (*Sitophilus zeamais* Motschulsky) is a major storage pest prevalent in all maize growing areas especially in tropical countries. Weevils usually begin infesting the maize grain in the field from where they begin multiplying and causing damage up to the processing stage (Demisse et al., 2008). The most economically and environmentally sustainable control measure against weevils, especially at smallholder farmer level is the use of host plant resistance (Dobie 1977). Deployment of weevil resistant maize cultivars would greatly minimize losses in grain quantity and quality arising from weevil infestations. However, most of the breeding strategies have been emphasizing grain yield and traits that directly contribute to yield enhancement. Considerable research has been conducted on grain yield enhancement (Tollenaar and Lee, 2006); grain yield and drought stress tolerance (Derera et al., 2007); grain yield, nitrogen-, and drought-stress tolerance (Makumbi et al., 2011); and grain yield and resistance to diseases (Vivek et al., 2010). There are only a few studies that have focused on grain improvement for weevil resistance. Hence there are few weevil resistant varieties that are available to the farmers in tropical environments.

Results from previous studies have shown that weevil resistance occurs in maize germplasm (Widstrom et al., 1972; Derera et al., 2001; García-Lara et al., 2009; Mwololo et al., 2010). Additionally, results from several studies have revealed the existence of high genetic variability for weevil resistance in a number of maize germplasm (Li et al., 1998; Siwale et al., 2009; Dari et al., 2010), which increases opportunities for maize germplasm enhancement towards weevil resistance. Therefore, identification and utilization of weevil resistant germplasm lines would be an important step in the development of weevil resistant maize cultivars. Most of the studies conducted on identifying sources of weevil resistance have mainly focused on grain resistance against weevils, but limited attention has been given to a combination of traits (Abebe et al., 2009; Mwololo et al., 2010). Thus, knowledge of the relationship between weevil resistance and grain yield, and maize reaction to foliar diseases would be important in the maize improvement strategies against weevil infestation. This is crucial because the end product must combine both pre and postharvest values to the farmers.

This study was conducted to determine the genetic variability for weevil resistance in maize germplasm lines from Uganda, Kenya and South Africa representing eastern and southern Africa. The inbred lines were also evaluated for yield and reaction to *Turcicum* leaf blight (TLB), grey leaf spot (GLS) and rust diseases which occurred during the study. The objectives of the

study were to: i) identify new sources of maize weevil resistance; ii) identify new sources of foliar diseases resistance iii) determine the genetic variation for weevil resistance; and iv) determine the association between weevil resistance and grain yield. The information would be useful in devising the most appropriate strategy for weevil resistance breeding in maize.

3.2 Materials and methods

3.2.1 Germplasm lines

For broadening the genetic base for weevil resistance, tropical and sub-tropical maize germplasm was used. The tropical germplasm was obtained from the National Crops Resources Research Institute (NaCRRI), Namulonge, Uganda (51 inbred lines) and the International Maize and Wheat Improvement Centre (CIMMYT), Kenya (55 inbred lines), while the sub-tropical germplasm (74 inbred lines) were sourced from the University of KwaZulu Natal, Republic of South Africa. The total number of inbred lines screened was 180, to which two weevil resistant checks [Genotype#10 [weevil/CML312]-B-13-2-1-BBB/[weevil/CML387]-B-9-1-1 (CIMMYT HA1091), and Genotype # 11 07WEEVIL (CIMMYT HA1091)], and two susceptible checks (local popcorn and Longe5) were added. The pedigree and origin of the study germplasm are given in Appendix 3.1.

3.2.2 Seed multiplication and field evaluation

The 180 inbred lines were planted in the first rainy season between March and June (season A), 2010 for seed increase and evaluation of their agronomic characteristics at the National Crops Resources Research Institute (NaCRRI), Namulonge (1200 m.a.s.l); 0°32'N, 32°34'E; 1300 mm bimodal rainfall. Another field evaluation trial was conducted at the site in the second rainy season from September to November (season B), 2010. The experimental design used was 18 x 10 alpha-lattice design, with two replications laid side by side. Single row plots of 5 m were used. The inter-row spacing was 0.75 m, while the intra-row spacing was 0.3 m. The weevil resistant and susceptible control hybrids were planted next to the evaluation trial, to avoid competition with the inbred lines. Di-ammonium phosphate (18% phosphorus) was applied at a rate of 120 kg/ha, at planting; while urea (46% nitrogen) was applied at a rate of 120 kg/ha 21 days after planting. To avoid out-crossing, the genotypes were sib-mated and covered with shoot bags until harvest.

3.2.3 Assessment of inbred lines for response to foliar diseases

The inbred lines were assessed for response to foliar diseases which accidentally occurred during yield evaluation of the lines; there was no artificial inoculation. The trial was scored for disease resistance towards physiological maturity, when plants are still green. A scale of 1 – 5, adopted from CIMMYT, was used to assess inbred line reaction to foliar diseases under natural infection. The scales were defined as follows: 1 = very slight to slight infection, one or two to few scattered lesions on lower leaves; 2 = light infection, moderate number of lesions on lower leaves only; 3 = moderate infection, abundant lesions on lower leaves, few on middle leaves; 4 = heavy infection, lesions abundant on lower and middle leaves, extending to upper leaves; 5 = very heavy infection, lesions abundant on almost all leaves, plants prematurely dry or killed by the disease.

3.2.4 Yield estimation

At physiological maturity the ears were harvested, dehusked and weighed for each genotype to determine the field weights. Furthermore, each genotype was sampled to obtain grain used for estimation of the moisture content (%), after which they were sun dried and prepared for screening against weevils. Remnant seed was kept for planting the second season trial. Grain yield (t ha^{-1}) was calculated for each genotype as follows:

$$\text{Grain Yield (t ha}^{-1}\text{)} = \left(\frac{(\text{Grain weight (kg/plot)}) \times 10 \times (100 - \text{MC})}{(100 - 12.5)(\text{Plot area})} \right) \times \text{shelling percentage};$$

where MC = grain moisture content (%).

3.2.5 Weevil culture rearing

Prior to the screening exercise, weevils were first multiplied (reared) to provide an adequate supply of age 0 to 7 days. This represented the first generation of laboratory reared weevils with known age. Weevil rearing was achieved by obtaining adult weevils from infested maize grain from nearby maize storage facilities. About 300 unsexed weevils were introduced into 1500 g of maize variety Longe5, one of the most susceptible maize varieties in Uganda, into large plastic jars of volume 3000 cm^3 (Figure 3.1a). To provide for proper ventilation, the lids of the plastic jars were perforated and gauze-wire mesh of pore size less than 1 mm stuck on them (lids) to prevent the weevils from escaping. The weevil-maize culture was incubated for 14 days in the

laboratory at a temperature of $28\pm 2^{\circ}\text{C}$ and a relative humidity of $70\pm 5\%$ to enhance oviposition. A heat fan and a humidifier were used for regulating the temperature and relative humidity, respectively. After two weeks the maize-weevil cultures were sieved using a mesh sieve (Endecotts Ltd, UK), to remove the weevils from the grain. The maize grain was later returned to the plastic jars and incubated under the same conditions, to allow the eggs to hatch and F_1 progenies to emerge. The grain of inbred lines was infested using these newly emerged F_1 progenies of age 0 to 7 days old.



a.

b.

Figure 3. 1: a. Mass rearing of the maize weevils in plastic jars; b. laboratory experimental layout.

3.2.6 Grain resistance test

The grain for screening against weevils was first subjected to cold treatment at -20°C for 14 days, to get rid of both adult and immature weevils that could have infested the grain in the field. After cold treatment the grain was acclimatized for seven days under a weevil free environment and later 50 g were weighed into glass jars of size 250 cm^3 . The grain in the glass jars was infested with 32 unsexed adult weevils that were reared as described in Section 3.2.5. The maize grain-weevil cultures were laid out in the laboratory in a randomized complete block design with three replications (Figure 3.1b). The cultures were incubated for oviposition for 14 days under controlled laboratory conditions as described above. After 14 days the parental weevils were sieved out of the maize grain to ensure that the weevils that subsequently emerged were only F_1 generation progenies. Seven days after parental weevil removal, the

cultures were monitored on a daily basis to observe for any F₁ weevil progeny emergence. On first appearance of the F₁ progenies, the cultures were then monitored every two days for recording and removing any new F₁ weevil progenies emerging from the grain. This continued until no new F₁ weevils were emerging from the grain after about 75 days.

3.2.7 Data collection

Data were recorded on the number of parental weevils alive and parental weevils dead (parental weevil mortality), taken after the oviposition period (14 days). The number of weevils that emerged from each genotype was counted every after two days, starting from the forth week after the weevil-grain culture initiation. The total number of F₁ weevil progenies that emerged per genotype was obtained by summing-up the weevils recorded per genotype. The median development period (MDP) of the maize weevil determined for each genotype was calculated as the time (days) from the middle of the oviposition period to the emergence of 50% of the F₁ weevil progenies (Dobie, 1977). Grain damage was calculated as the percentage of damaged grains over total grains per sample.

Dobie's index of susceptibility (DIS) was calculated based on the total F₁ weevil emergence and the median development period for each genotype (Dobie, 1974). It was calculated using the formula:

$$\text{DIS} = \log_e (\text{Number of F}_1 \text{ weevil progeny emergence}) / (\text{Median Development Period}) \times 100$$

Where \log_e = natural logarithms

3.2.8 Data analysis

The grain susceptibility parameters analyzed were: number of parental weevils alive, parental weevil mortality, total F₁ weevil progeny emerged, the median development period and percent grain damage. The parameters were subjected to the "general linear models" of SAS version 9.1 (SAS-Institute, 2003). The differences between means were detected using least significant differences at a 5% probability level (LSD = 0.05). Similarly, the field data on grain yield and reaction of inbred lines to *Turcicum* leaf blight (TLB), grey leaf spot (GLS) and rust for the two seasons (2010A and 2010B) were subjected to the same analyses.

Heritability was estimated using genotypic and environmental variance components of the study traits (Hallauer and Miranda, 1988). The variance components were estimated using the REML tool in GenStat version 14 (Payne et al., 2011). During analysis, the genotypes were considered as random effects, while the replications were considered as fixed effects. Heritability was estimated from the formula:

$$h^2 = Vg / [(Ve/rs) + Vg] \times 100$$

where Vg = genotypic variance; Ve = environmental variance; r = number of replications; s = number of sites.

Data on inbred line response to weevil infestation using Dobie's index of susceptibility (DIS) were regressed against grain yield and inbred line reaction to TLB, GLS, and rust to generate scatter plots.

3.2.9 Categorization of inbred lines

Parameters: F₁ weevil progeny emergence (FWE), percent grain damage (GD), median development period (MDP), and Dobie's index of susceptibility (DIS) were used to categorize inbred lines into various weevil response classes (resistant, moderately resistant, moderately susceptible, susceptible and highly susceptible). Based on Dobie (1974) index of susceptibility, the 180 inbred lines were allocated into five response classes. The response classes were defined as 1.0 – 4.0 = resistant, 4.1 – 7.0 = moderately resistant, 7.1 – 10.0 = moderately susceptible, 10.1 – 13.0 = susceptible, and ≥13.1 = highly susceptible. For the other parameters (F₁ weevil progeny emergence, percent grain damage and median development period), grouping of the inbred lines was based on the response of the resistant and susceptible control check varieties, the least significant differences (LSD) and the trial mean. Inbred lines with data that were not significantly different from the resistant checks were regarded as resistant. Inbred lines with values that were significantly lower than the trial mean but higher than the resistant check were classified as moderately resistant; inbred lines with responses not significantly different from the trial mean were categorized as moderately susceptible. The inbred lines with values that were significantly higher than the trial mean, and those that were not significantly different from the susceptible check were fitted in the susceptible class.

3.3 Results

3.3.1 Genotypic variation

The mean squares for five grain susceptibility parameters are shown in Table 3.1. The mean squares for percent grain damage (GD), Dobie's index of susceptibility (DIS), F₁ weevil progeny emergence (FWE), and median development period (MDP) indicated that genotypes and environments were significant ($0.05 > P < 0.001$), while for parental weevil mortality (PWM), all effects and interactions were not significant ($P > 0.05$). Environment x genotype interactions were significant for percent grain damage ($P < 0.001$) and DIS ($P < 0.05$), whereas they were not significant ($P > 0.05$) for F₁ weevil emergence, median development period and parental weevil mortality.

Table 3. 1: Mean squares for grain susceptibility parameters for the 180 inbred lines and four checks

Source	DF	Mean Square				
		FWE	GD	MDP	DIS	PWM
Env	1	40261.68***	191.1***	74.09*	72.09***	79.90
Rep	2	67910.63	1003.58	1891.05	695.21	52.14
Genotype	183	7145.64***	82.38***	203.87***	58.43***	73.30
Env*Genotype	183	677.96	6.06***	11.96	2.32*	69.17
Error	734	701.68	4.29	13.74	1.88	26.32
R²		0.76	0.85	0.81	0.90	0.58
CV (%)		40.20	12.61	9.82	12.65	51.08

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively, and ns indicate not significant at 5% probability level, FWE = F₁ weevil progeny emergence, GD = Percent grain damage, MDP = median development period, DIS = Dobie index of susceptibility, PWM = parental weevil mortality.

Results for the mean response of the 20 most weevil resistant and five most susceptible inbred lines, together with the two resistant checks (genotypes RC181 and RC182), and two susceptible checks (genotypes SC183 and SC184) as revealed by F₁ weevil emergence, percent grain damage, median development period and Dobie's index of susceptibility are shown in Table 3.2. The results indicated significant ($P < 0.05$) differences among inbred lines for the four grain susceptibility parameters. Inbred lines MV13, MV21, MV23, MV31, MV63, MV75, MV102, MV105, MV142, MV154, MV157, MV170, and MV175 were grouped among the 20 most weevil resistant inbred lines by the four susceptibility parameters.

Table 3.2: Mean responses of the 20 top weevil resistant and 5 most susceptible inbred lines compared to the resistant and susceptible checks, as revealed by four grain susceptibility parameters.

Checks	Genotype	FWE	Genotype	GD	Genotype	MDP	Genotype	DIS
Top 20	MV165	5.7	MV170	8.2	MV31	52.0	M170	3.2
	MV170	5.8	MV75	8.4	MV170	52.0	MV75	3.4
	MV75	6.7	MV157	8.7	MV21	51.7	MV157	3.7
	MV102	7.0	MV21	8.7	MV154	51.3	MV21	3.7
	MV142	7.0	MV142	8.8	MV23	51.0	MV142	3.8
	MV157	7.0	MV102	8.8	MV63	50.7	MV102	3.8
	MV21	7.3	MV23	9.0	MV75	50.3	MV23	4.0
	MV23	7.8	MV31	9.0	MV178	50.2	MV31	4.0
	MV63	8.0	MV63	9.0	MV157	49.7	MV63	4.0
	MV154	8.2	MV154	9.1	MV102	49.3	MV154	4.1
	MV31	9.5	MV165	9.1	MV169	49.3	MV165	4.1
	MV105	9.7	MV105	9.4	MV105	49.0	MV105	4.4
	MV175	10.5	MV13	9.5	MV144	48.8	MV13	4.5
	MV13	10.7	MV175	9.8	MV177	48.3	MV175	4.8
	MV12	11.2	MV163	10.6	MV182	48.3	MV163	5.6
	MV163	13.5	MV169	10.7	MV174	48.2	MV169	5.7
	MV159	14.0	MV159	10.8	MV6	48.0	MV159	5.8
	MV19	14.2	MV177	10.8	MV13	48.0	MV177	5.8
	MV168	15.0	MV168	10.9	MV142	47.7	MV168	5.9
	MV164	16.7	MV174	10.9	MV175	47.3	MV174	5.9
Resistant checks	RC182	8.0	RC182	8.2	RC182	50.0	RC182	3.7
	RC181	7.2	RC181	9.3	RC181	48.3	RC181	3.2
Bottom 5								
	MV88	120.2	MV83	22.2	MV155	30.0	MV78	14.8
	MV104	130.7	MV100	22.3	MV41	29.7	MV33	14.8
	MV33	132.8	MV44	22.8	MV90	29.7	MV138	15.1
	MV83	143.7	MV33	23.2	MV138	29.7	MV9	15.4
	MV44	151.5	MV9	23.7	MV2	29.3	MV41	15.6
Susceptible checks	SC183	113.3	SC183	24.9	SC183	32.3	SC183	15.5
	SC184	132.7	SC184	23.0	SC184	30.5	SC184	14.1
LSD (0.05%)		30.0		2.3		4.2		1.5
Trial mean		65.7		16.4		37.8		10.8

FWE = F1 weevil progeny emergence, GD = Percent grain damage, MDP = median development period, and DIS = Dobie index of susceptibility.

Results indicated that the number of F_1 weevil progenies that emerged from the grain of the 20 most resistant inbred lines were not significantly ($P < 0.05$) different from those that emerged from the resistant check. Inbred lines MV21, MV23, MV75, MV102, MV142, MV157, MV165, and MV170 supported fewer F_1 weevil progenies, but were not significantly different from those of the resistant check. The smallest mean number of F_1 weevil progeny emergence was 5.67, exhibited by inbred line MV165, while the largest mean number of F_1 weevil progenies was 151.50 exhibited by inbred line MV44. The two most susceptible genotypes, MV44 and MV83, supported a significantly ($P < 0.05$) higher number of F_1 weevil progenies than the susceptible check.

Regarding percent grain damage, the least grain damage was 8.20%, exhibited in inbred line MV170; whilst the highest damage was 23.74%, encountered by inbred line MV9. The responses of the 14 most resistant inbred lines namely MV13, MV21, MV23, MV31, MV63, MV75, MV102, MV105, MV142, MV154, MV157, MV165, MV170, and MV175 did not significantly ($P < 0.05$) differ from that of the resistant check. The damage exhibited in the three most susceptible inbred lines did not significantly differ from that of the susceptible check. For the median development period, it ranged from 29.33 days in a susceptible inbred line MV2, to 52 days in the resistant inbred line MV170. All the 20 most weevil resistant inbred lines, shown in Table 3.2, were not significantly ($P < 0.05$) different from the resistant check. Inbred lines MV21, MV23, MV31, MV63, MV75, MV154, MV170, and MV178 exhibited longer median development periods, but were not significantly ($P > 0.05$) different from the resistant check. The five most susceptible inbred lines, (MV2, MV41, MV90, MV138, and MV155) were also not significantly ($P > 0.05$) different from the susceptible check. As regards the Dobie's index of susceptibility, the lowest value was 3.20 manifested in inbred line MV170, while the largest index was 15.61, exhibited by inbred line MV41. Values for inbred lines MV13, MV21, MV23, MV31, MV63, MV75, MV102, MV105, MV142, MV154, MV157, MV170, and MV175 were not significantly ($P < 0.05$) different from that of the resistant check. Similarly, values for the five most susceptible inbred lines MV9, MV33, MV41, MV78, and MV138 were not significantly different from the susceptible check value.

3.3.2 Frequency distribution of inbred lines

Results for the distribution of the 180 inbred lines into different response classes as grouped by F_1 weevil progeny emergence, percent grain damage, median development period, and Dobie's

index of susceptibility are shown in Figure 3.1: a, b, c and d, respectively. The results of the F_1 weevil progeny emergence (Figure 3.1: a) showed that 35 inbred lines were not significantly ($P < 0.05$) different from the resistant check and hence were categorized in the resistant class (0.0 – 30.0 F_1 weevil progenies). Forty inbred lines were grouped in the moderately resistant class (30.1 – 60.0, F_1 weevil progenies), 60 inbred lines were grouped in the moderately susceptible class (60.1 – 90.0), while 46 inbred lines were grouped in the susceptible class (≥ 90.1). The distribution of inbred lines into the four response categories exhibited a normal distribution trend with the majority of inbred lines (60) being in the moderately susceptible class under which the trials mean (65.7 weevils) fell. The resistant and susceptible checks were noted to fall under their respective, resistant and susceptible classes, with fewer inbred lines than the moderately resistant and moderately susceptible classes.

Results of the percent grain damage (Figure 3.1: b) exhibited the same trend as that of F_1 weevil progeny emergence. Fourteen inbred lines encountered grain damage that was not significantly different from the resistant check and were hence grouped in the resistant class (6.0 – 11.0% damage). Fifty six inbred lines were grouped in the moderately resistant class (11.1 – 16.0%), 99 inbred lines were grouped in the moderately susceptible class (16.1 – 21.0%), while 11 inbred lines were grouped in the susceptible class (21.1 – 26.0%). The distribution of inbred lines exhibited a trend close to a normal distribution curve, with the majority of inbred lines falling under the moderately resistant and moderately susceptible classes under which the trials mean (16.42% damage) was. The resistant and susceptible checks fell under the resistant- and susceptible-classes, respectively, under which fewer inbred lines were fitted than in the moderately resistant and moderately susceptible classes.

For the median development period (Figure 3.1: c), 20 inbred lines were grouped in the resistant class (47.0 – 53.0 days), 25 inbred lines were grouped in the moderately resistant class (41.1 – 47.0 days), 57 inbred lines were grouped in the moderately susceptible class (35.1 – 41.0 days), while 78 inbred lines were grouped in the susceptible class (29.0 – 35.0 days). Here the distribution of inbred lines into various response classes was skewed to the left, where the majority of inbred lines (78) with short median development periods fell. The susceptible check fell in the susceptible class where the majority of inbred lines were fitted. The resistant check on the other hand, was fitted in the resistant class with the least number of inbred lines that exhibited the longest median development periods.

Results of the Dobie's index of susceptibility (Figure 3.1: d), exhibited an inverse trend to that of the MDP, with the inbred lines that exhibited longer MDPs displaying smaller indices, while those with shorter MDPs displayed larger indices. Consequently, eight inbred lines with indices 1.0 – 4.0 were categorized as resistant, 19 inbred lines were categorized as moderately resistant (4.1 – 7.0); 34 were categorized as moderately susceptible (7.1 – 10.0); 65 inbred lines were categorized as susceptible (10.01 – 13.0); while 54 inbred lines were categorized as highly susceptible. The distribution of inbred lines into the various response classes was generally normal, although it was tending to skew towards to the right, where inbred lines with DIS values above 10.0 (susceptible) were fitted. The resistant check was fitted in the resistant class with the least number of inbred lines (eight); while the susceptible check fell in the susceptible class with the second biggest number of inbred lines (54).

3.3.3 Distribution of inbred lines based on their response classes and origin

The summary for the distribution of 180 inbred lines with respect to their origin and weevil susceptibility classes, as grouped by Dobie's susceptibility index, is shown in Table 3.3. A number of inbred lines were consistently grouped into the same response classes by the four grain susceptibility parameters (Table 3.2). Therefore, only one parameter, Dobie's index of susceptibility, was considered when allocating inbred lines into different response classes based on their origins (Table 3.3). The results indicated that all susceptibility classes were exhibited in germplasm from Uganda, CIMMYT-Kenya and South Africa. At least 7.8% of the inbred lines from Uganda were resistant, compared to 3.6% and 2.7% of the lines from CIMMYT-Kenya and South Africa, respectively. On the overall, only 4.4% of the total samples of 180 inbred lines displayed resistance to the maize weevil, and were hence categorized in the resistant class. Inbred lines fitted in the moderately resistant class constituted 10.6%, inbred lines that fell under moderately susceptible constituted 18.9%, inbred lines that were grouped as susceptible constituted 36.1%, while 30% of the inbred lines were categorized as highly susceptible.

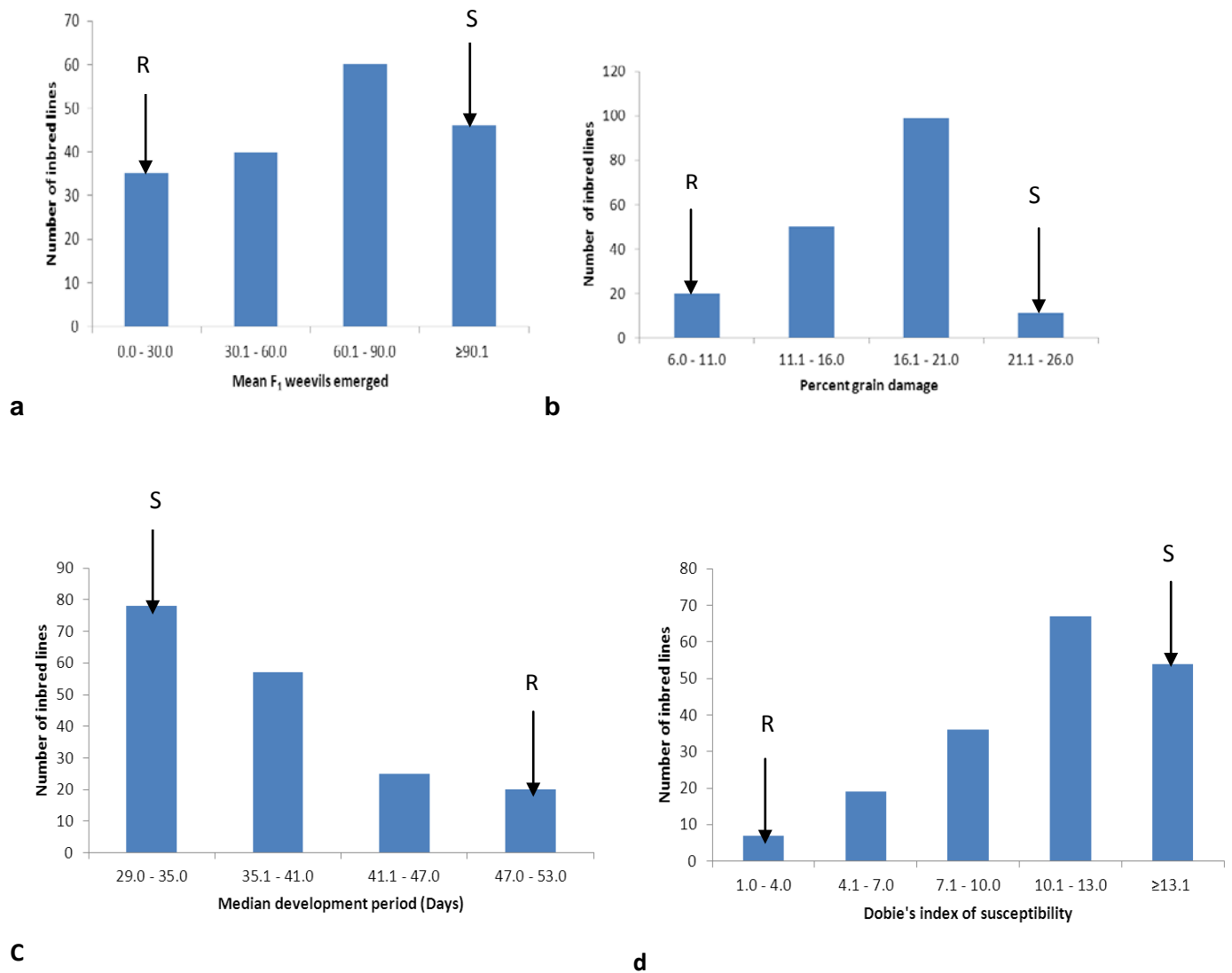


Figure 3.2: Frequency distribution of 180 inbred lines into different weevil susceptibility classes as grouped by the four grain susceptibility parameters: a) F₁ weevil progeny emergence; b) percent grain damage; c) median development period; d) Dobie index of susceptibility. The arrows indicate the classes where the resistant (R) and susceptible (S) checks fell.

On the overall, only 4.4% of the total samples of 180 inbred lines displayed resistance to the maize weevil, and were hence categorized in the resistant class. Inbred lines fitted in the moderately resistant class constituted 10.6%, inbred lines that fell under moderately susceptible constituted 18.9%, inbred lines that were grouped as susceptible constituted 36.1%, while 30% of the inbred lines were categorized as highly susceptible.

Table 3.3: Distribution of inbred lines from Uganda, CIMMYT-Kenya, and South Africa into different weevil susceptibility classes as categorized by Dobie index of susceptibility

Class	Uganda		CIMMYT-Kenya		South Africa		Overall total	
	No.	%	No.	%	No.	%	No.	%
1.0 – 4.0	4	7.8	2	3.6	2	2.7	8	4.4
4.1 – 7.0	13	25.5	5	9.1	1	1.4	19	10.6
7.1 – 10.0	16	31.4	13	23.6	5	6.8	34	18.9
10.1 – 13.0	14	27.5	15	27.3	36	48.6	65	36.1
≥13.1	4	7.8	20	36.4	30	40.5	54	30.0
Total	51		55		74		180	

3.3.4 Heritability estimates

The narrow sense heritability estimates for F₁ weevil progeny emergence, percent grain damage, median development period, Dobie's index of susceptibility, grain yield, *Turcicum* leaf blight, rust and grey leaf spot diseases are shown in Table 3.4. The genetic variances for F₁ weevil progeny emergence (FWE), percent grain damage (GD), median development period (MDP) and Dobie index of susceptibility (DIS) were large relative to their respective environmental variances. Consequently, they all portrayed high heritability estimates above 89%. The genetic variances for yield and *Turcicum* leaf blight were moderate, and hence they exhibited moderately high heritability estimates of 58% and 40%, respectively. On the other hand, the low heritability estimates exhibited by the rust and grey leaf spot disease parameters were attributed to the generally small genetic variances relative to the environmental variances.

Table 3.4: Narrow sense heritability estimates for the four grain susceptibility parameters, grain yield and three foliar diseases exhibited in the 180 inbred lines

Variance component	Means \pm SE							
	FWE	GD	MDP	DIS	Yield	TLB	Rust	GLS
Vg	1032.0 \pm 121.6	11.9 \pm 1.34	30.56 \pm 3.47	8.81 \pm 0.97	0.03 \pm 0.01	0.02 \pm 0.01	0.003 \pm 0.01	0.004 \pm 0.01
Ve	700.10 \pm 33.1	4.63 \pm 0.22	13.54 \pm 0.64	1.94 \pm 0.09	0.12 \pm 0.01	0.16 \pm 0.01	0.50 \pm 0.02	0.67 \pm 0.03
h²	89.84\pm	93.92\pm	93.12\pm	96.45\pm	58.28\pm	40.53\pm	3.90\pm	3.65\pm

FWE = F₁ weevil progeny emergence, GD = Percent grain damage, MDP = median development period, and DIS = Dobie index of susceptibility, TLB = *Turicum* leaf blight, GLS = grey leaf spot.

3.3.5 Relationship between weevil resistance, grain yield and reaction to *Turcicum* leaf blight, grey leaf spot and rust

The relationships between Dobie's index of susceptibility with grain yield, *Turcicum* leaf blight, grey leaf spot, and rust are shown in Figure 3.2. The four scatter plots exhibited the same trend, with low R^2 values and the scatter points distributed along (parallel) the X-axis.

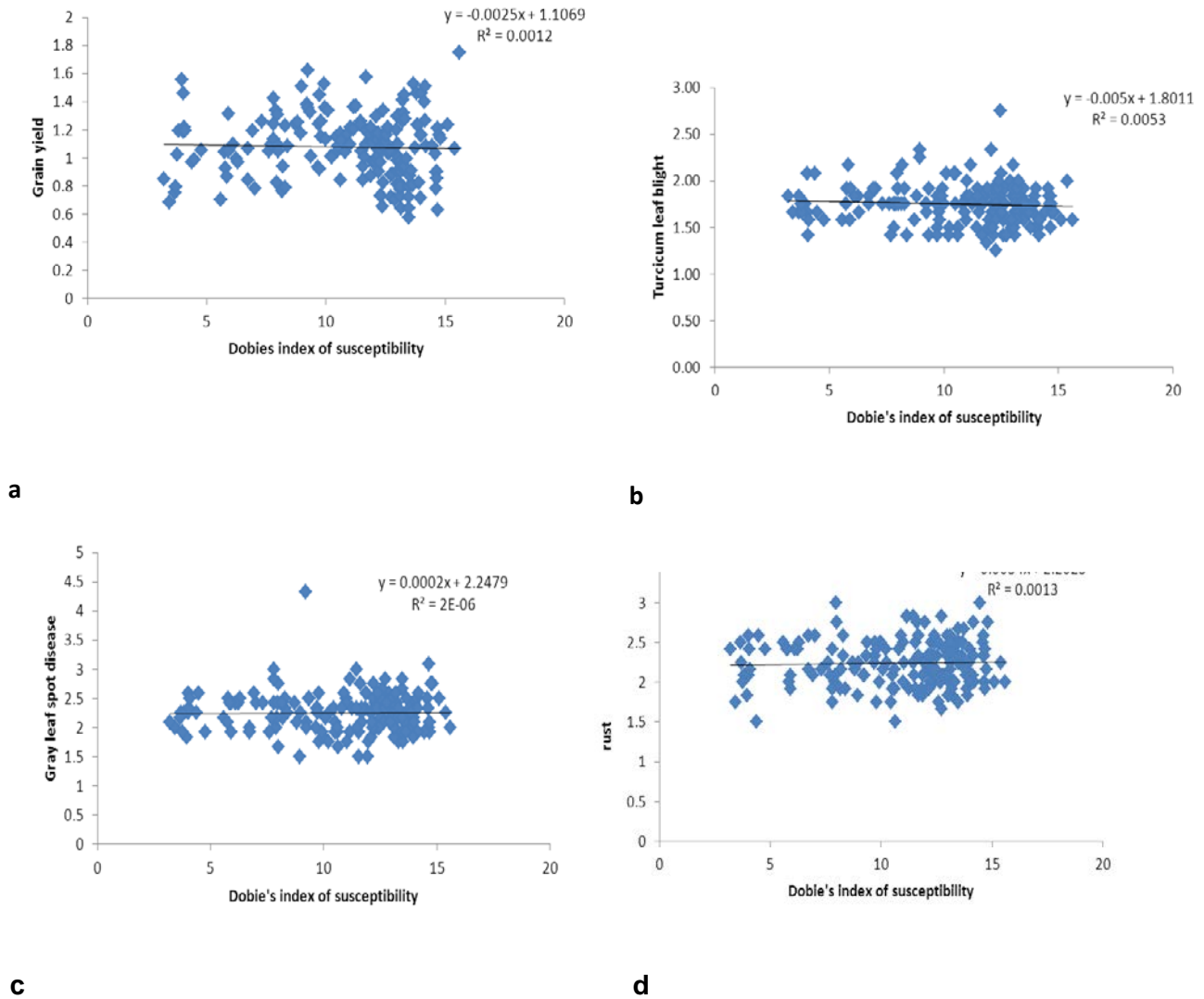


Figure 3. 3: Scatter plots for the relationships between Dobie index of susceptibility with other traits. a: relationship with grain yield, b: relationship with *Turcicum* leaf blight, c: relationship with grey leaf spot, and d: relationship with rust.

3.4 Discussion

3.4.1 Genotype response to weevil infestation

The significant environments portrayed by the mean squares for F₁ weevil progeny emergence, percent grain damage, median development period and Dobie's index of susceptibility indicated that the differences among the inbred lines were partly attributed to the differences in the two seasons under which the trial was conducted (Li et al., 1998). On the other hand, the significant genotype mean squares demonstrated by F₁ weevil progeny emergence, percent grain damage, median development period and Dobie's index of susceptibility indicated that the 180 inbred lines exhibited genetic variations for weevil resistance. The existence of genetic variations for weevil resistance in maize germplasm from eastern and southern African region suggested a high potential for introduction of new sources of weevil resistance that can be exploited for subsequent development of weevil resistant maize cultivars. Genetic variations for weevil resistance have been observed in various maize germplasm including hybrids and open pollinated varieties (Li et al., 1998; Mwololo et al., 2012; Widstrom et al., 1983).

The significant environment x genotype interactions for percent grain damage and Dobie's index of susceptibility suggested differences in genotype response to weevil infestations between seasons. The differences in genotype response could be attributed to the differences in grain characteristics, that might be manifested as a result of changes in the environment. For example, grain characteristics like texture, and to some extent, kernel hardness might be affected by drought, which can limit grain filling and this would consequently affect grain texture and/or hardness. Manifestation of significant environment x genotype interactions is consistent with observations by Tipping et al. (1989).

The mean square results further indicated that grain susceptibility parameters: F₁ weevil progeny emergence, percent grain damage, median development period and Dobie's index of susceptibility were able to discriminate the inbred lines based on their variations in weevil susceptibility (Abebe et al., 2009). However, parental weevil mortality as a weevil susceptibility parameter, did not detect significant ($P < 0.05$) differences in weevil resistance among the 180 test inbred lines, nor could it detect differences among other effects and environment x genotype interactions. This implied that parental weevil mortality was not a suitable parameter for discriminating maize cultivars for weevil resistance.

3.4.2 Inbred distribution into different weevil susceptibility classes

The distribution of inbred lines into the different response classes exhibited a “generally” continuous (normal) distribution (Figure 3.1: a, b, and d), implying that weevil resistance is controlled by quantitative genes; hence breeding procedures that exploit polygenes and quantitative trait loci QTLs would be recommended in breeding for weevil resistance. It was observed that in the resistant inbred lines, a fewer number of F_1 weevil progenies emerged, and these took a longer period to emerge, as opposed to the susceptible inbred lines which encountered more F_1 weevil progeny emergence in a shorter period. These results indicated that there could be some factors in the resistant grain that delay progeny growth and development as shown by the significantly lower number of F_1 weevil progenies and longer MDP for the resistant and susceptible inbred lines. Antibiosis could be one of the factors responsible for the resistance manifested in the study germplasm (Derera et al., 2001; García-Lara et al., 2007). Therefore, analysis of some of the resistant and susceptible inbred lines for the levels of biochemical compounds such as phenolics and peroxidases, responsible for antibiosis, would be necessary to confirm the occurrence of antibiosis for the resistance observed. García-Lara et al. (2009) reported higher concentrations of peroxidases and phenolic compounds in weevil resistant maize genotypes than susceptible ones.

The results from the four weevil screening parameters (F_1 weevil emergence, percent grain damage, median development period and Dobie’s index of susceptibility) grouped similar inbred lines in the same susceptibility classes. This implied that the four grain susceptibility parameters were consistent in discriminating the inbred lines. Inbred lines MV13, MV21, MV23, MV31, MV63, MV75, MV102, MV105, MV142, MV154, MV157, MV170, and MV175 were grouped among the 20 most weevil resistant inbred lines by the four susceptibility parameters used in the study. Weevil resistant inbred lines that were not significantly different from the resistant checks will be potential parents for development of weevil resistant maize cultivars. Thus, inbred lines MV142, MV154, MV157, and MV170 from Uganda; inbred lines MV21 and MV23 from CIMMYT-Kenya; and inbred lines MV75 and MV102 from South Africa that were consistently grouped in the resistant categories and portrayed good performances comparable to the resistant check will be potential parents for breeding new varieties. The existence of weevil resistant inbred lines together with those in different susceptibility classes demonstrated high genetic variability in the study germplasm. This suggested an opportunity for broadening the genetic base for weevil resistance, since the inbred lines were from three different geographical

areas, which may imply differences in the sources of resistance. However, further tests involving molecular markers would be recommended to verify whether these materials are genetically different.

3.4.3 Heritability

The large heritability values (above 89%) for weevil resistance, as exhibited by F_1 weevil progeny emergence, percent grain damage, median development period and Dobie's index of susceptibility implied that a greater proportion of the phenotypic expression of the inbred lines was contributed by the genotypic variance. Thus there was minimal environmental variance that was influencing the four grain susceptibility parameters/grain resistance against weevil infestations in the inbred lines. The large heritability manifested in the four parameters suggested that selection would be effective in improving the germplasm towards weevil resistance. The large heritability values for the susceptibility parameters are consistent with García-Lara et al. (2010) who reported up to 79% heritability of weevil resistant molecular traits. Grain yield exhibited moderate heritability indicating that selection would be quite effective towards improving grain yield in the germplasm. The low heritability exhibited for *Turcicum* leaf blight, rust, and grey leaf spot diseases was because there were no inoculations, and hence their manifestation was a result of natural infection. The low heritability suggested that selection would be less effective in improving the study inbred lines against the three diseases, unless the disease pressure is augmented through artificial inoculations.

Regarding the association between Dobie's index of susceptibility and grain yield, and also with *Turcicum* leaf blight, grey leaf spot, and rust, the small R^2 values (<1.0%) and the parallel distribution of coordinates along the X-axis, manifested in the scatter plots indicated insignificant associations between these traits. This suggested that improvement of the study germplasm for weevil resistance would not necessarily comprise yield and resistance against *Turcicum* leaf blight, grey leaf spot, and rust. These results provide evidence that maize improvement for weevil resistance may not necessarily comprise yield and foliar disease resistance.

3.5 Conclusion

The results indicated that high genetic variability existed in the study germplasm. Inbred lines MV21, MV23, MV75, MV102, MV142, MV154, MV157, and MV170, that were categorized as resistant will be new good sources of weevil resistance which can be exploited to breed new

varieties, and thus they are recommended for utilization in subsequent weevil breeding programs. Observation of high heritability (h^2) means selection would be effective in germplasm improvement for maize weevil resistance. Accordingly, the possibility of broadening the gene pool for weevil resistance and yield ought to be explored, for instance through gene pyramiding. However, molecular studies would be necessary, to ascertain whether the resistance exhibited in the three sources of germplasm were actually from different genetic backgrounds. The insignificant association between maize weevil resistance and grain yield suggested that improvement for weevil resistance can be executed without associated reduction in grain yield. Findings from this study would be crucial for breeding programmes that aim at emphasizing maize weevil resistance in maize.

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Appendix 3.1: Genotype numbers and origin of inbred lines used in screening for weevil resistance

Genotype No.	Pedigree/designation	Origin
MV1	CKL05001	CIMMYT-Kenya
MV2	CKL05002	CIMMYT-Kenya
MV3	CKL05004	CIMMYT-Kenya
MV4	CKL05006	CIMMYT-Kenya
MV5	CKL05007	CIMMYT-Kenya
MV6	CKL05009	CIMMYT-Kenya
MV7	CKL05010	CIMMYT-Kenya
MV8	CKL05013	CIMMYT-Kenya
MV9	CKL05014	CIMMYT-Kenya
MV10	CKL05015	CIMMYT-Kenya
MV11	CKL05016	CIMMYT-Kenya
MV12	CKL05018	CIMMYT-Kenya
MV13	CKL05019	CIMMYT-Kenya
MV14	CKL05020	CIMMYT-Kenya
MV15	CKL05021	CIMMYT-Kenya
MV16	CKL05022	CIMMYT-Kenya
MV17	CKL05023	CIMMYT-Kenya
MV18	CKL05024	CIMMYT-Kenya
MV19	CML505	CIMMYT-Kenya
MV20	CML509	CIMMYT-Kenya
MV21	CML507	CIMMYT-Kenya
MV22	CKL05025	CIMMYT-Kenya
MV23	ZEWA _c 1F ₂ -134-4-1-B-1-B*4-1-B-B-B	CIMMYT-Kenya
MV24	ZEWA _c 1F ₂ -254-2-1-B-1-BB-1-B-B-B	CIMMYT-Kenya
MV25	ZEWA _c 1F ₂ -80-1-1-B-1-B*4-1-B-B-B	CIMMYT-Kenya
MV26	ZEWA _c 1F ₂ -134-4-1-B-1-B*4-B-B	CIMMYT-Kenya
MV27	ZEWA _c 1F ₂ -300-2-2-B-1-B*4-B-B	CIMMYT-Kenya
MV28	[CML312/CML445//[TUXPSEQ]C1F2/MV449-SR]F2-45-3-2-1-BBB]-1-2-1-1-1-BBB-B-B-B	CIMMYT-Kenya
MV29	[CML312/MAS[MSR/312]-109-3]-B-71-3-BBB-B-B-B	CIMMYT-Kenya
MV30	[CML442/CML197//[TUXPSEQ]C1F2/MV449-SR]F2-45-7-3-2-BBB]-2-1-1-2-2-BBB-B-B-B	CIMMYT-Kenya
MV31	[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-B//EV7992/EV8449...-3-2-2-1-BBBBB-B-B-B	CIMMYT-Kenya
MV32	[CML395/CML444//ZM521B-66-4-1-1-1-BB]-4-2-1-1-B-B-B	CIMMYT-Kenya
MV33	[CML444/CML395//ZM521B-66-4-1-1-1-BB]-3-3-1-1-B-B-B	CIMMYT-Kenya

Appendix 3.1: continued

Genotype No.	Pedigree/designation	Origin
MV34	[CML440/[[[K64R/G16SR]-39-1/[K64R/G16SR]-20-2]-5-1-2-B*4/CML390]-B-39-2-B-4-#-1-B//ZM303c1-243-3-B-1-1-B]-9-1-B-B	CIMMYT-Kenya
MV35	[CML440/[[[K64R/G16SR]-39-1/[K64R/G16SR]-20-2]-5-1-2-B*4/CML390]-B-38-1-B-7-#-B//ZM303c1-243-3-B-1-1-B]-6-B-B	CIMMYT-Kenya
MV36	[CML440/[[[K64R/G16SR]-39-1/[K64R/G16SR]-20-2]-5-1-2-B*4/CML390]-B-38-1-B-7-#-B//ZM303c1-243-3-B-1-1-B]-2-1-B-B	CIMMYT-Kenya
MV36	[CML440/[[[K64R/G16SR]-39-1/[K64R/G16SR]-20-2]-5-1-2-B*4/CML390]-B-38-1-B-7-#-B//ZM303c1-243-3-B-1-1-B]-2-1-B-B	CIMMYT-Kenya
MV37	[CML440/[[[K64R/G16SR]-39-1/[K64R/G16SR]-20-2]-5-1-2-B*4/CML390]-B-38-1-B-7-#-B//ZM303c1-243-3-B-1-1-B]-1-1-B-B	CIMMYT-Kenya
MV37	[CML440/[[[K64R/G16SR]-39-1/[K64R/G16SR]-20-2]-5-1-2-B*4/CML390]-B-38-1-B-7-#-B//ZM303c1-243-3-B-1-1-B]-1-1-B-B	CIMMYT-Kenya
MV38	[CML440/[[[K64R/G16SR]-39-1/[K64R/G16SR]-20-2]-5-1-2-B*4/CML390]-B-38-1-B-7-#-B//ZM303c1-243-3-B-1-1-B]-1-2-B-B	CIMMYT-Kenya
MV39	[CML440/[[[NAW5867/MV310SR]-111-2/[NAW5867/MV310SR]-25-1]-9-2-3-B-2-B/CML388]-B-35-2-B-1-#-1//ZM303c1-243-3-B-1-1-B]-2-1-B-B	CIMMYT-Kenya
MV40	ZM521B-66-4-1-1-BB-B-B-B-B	CIMMYT-Kenya
MV41	CML536	CIMMYT-Kenya
MV42	MAS[MSR/312]-117-2-2-1-B*3-B-B	CIMMYT-Kenya
MV43	[CML444/ZSR923S4BULK-2-2-X-X-X-X-1-BB]-1-1-1-2/CML441]-1-1-1-2-B*4-B-B	CIMMYT-Kenya
MV44	[(CML395/CML444)-B-4-1-3-1-B/CML444/[TUXPSEQ]C1F2/MV449-SR]F2-45-7-1-2-BBB]-2-1-2-2-BBB-B-B-B	CIMMYT-Kenya
MV45	CML442-B	CIMMYT-Kenya
MV46	CML443-B	CIMMYT-Kenya
MV47	CML444-B	CIMMYT-Kenya
MV48	MV3100C5S1B-2-2-3-#-#1-2-B-B-B-B-B-B-B	CIMMYT-Kenya
MV49	SW89300-1MV13S2-5-#-#1-1-B-B-B-B-B-B-B	CIMMYT-Kenya
MV50	SW89300-1MV31S2-1-#-#1-8-B-B-B-B-B-B-B	CIMMYT-Kenya
MV51	CML395-B	CIMMYT-Kenya
MV52	CML440-B	CIMMYT-Kenya
MV53	CML445-B	CIMMYT-Kenya
MV54	CML488-B	CIMMYT-Kenya
MV55	CML489-B	CIMMYT-Kenya
MV56	09MAK17-12-1	South Africa
MV57	09MAK9-94	South Africa
MV58	09MAK17-4-1	South Africa
MV59	09MAK17-5-1	South Africa
MV60	09MAK17-6-1	South Africa

Appendix 3.1: continued

Genotype No.	Pedigree/ designation	Origin	Genotype No.	Pedigree/ designation	Origin
MV61	09MAK17-3-1	South Africa	MV98	09MAK7-72	South Africa
MV62	09MAK17-27-1	South Africa	MV99	09MAK7-64	South Africa
MV63	09MAK17-15-1	South Africa	MV100	09MAK17-1-1	South Africa
MV64	09MAK17-8-1	South Africa	MV101	09MAK7-37	South Africa
MV65	09MAK17-17-1	South Africa	MV102	09MAK9-157	South Africa
MV66	09MAK17-11-1	South Africa	MV103	09MAK9-113	South Africa
MV67	09MAK7-32	South Africa	MV104	09MAK17-44-1	South Africa
MV68	09MAK17-14-1	South Africa	MV105	09MAK17-9-1	South Africa
MV69	09MAK17-16-1	South Africa	MV106	09MAK9-35	South Africa
MV70	09MAK9-130	South Africa	MV107	09MAK9-47	South Africa
MV71	09MAK9-196	South Africa	MV108	09MAK7-47	South Africa
MV72	09MAK9-4	South Africa	MV109	09MAK7-82	South Africa
MV73	09MAK9-120	South Africa	MV110	09MAK17-2-1	South Africa
MV74	09MAK9-9	South Africa	MV111	09MAK17-40-1	South Africa
MV75	09MAK17-28-1	South Africa	MV112	09MAK17-42-1	South Africa
MV76	09MAK9-20	South Africa	MV113	09MAK17-41-1	South Africa
MV77	09MAK17-36-1	South Africa	MV114	09MAK7-19	South Africa
MV78	09MAK17-37-1	South Africa	MV115	09MAK7-6	South Africa
MV79	09MAK17-43-1	South Africa	MV116	09MAK17-33-1	South Africa
MV80	09MAK17-45-1	South Africa	MV117	09MAK17-18-1	South Africa
MV81	09MAK17-48-1	South Africa	MV118	09MAK17-53-1	South Africa
MV82	09MAK17-50-1	South Africa	MV119	09MAK17-29-1	South Africa
MV83	09MAK17-38-1	South Africa	MV120	09MAK17-13-1	South Africa
MV84	09MAK17-49-1	South Africa	MV121	09MAK17-32-1	South Africa
MV85	09MAK17-47-1	South Africa	MV122	09MAK17-7-1	South Africa
MV86	09MAK17-46-1	South Africa	MV123	09MAK17-20-1	South Africa
MV87	09MAK17-39-1	South Africa	MV124	09MAK17-24-1	South Africa
MV88	09MAK17-30-1	South Africa	MV125	09MAK17-22-1	South Africa
MV89	09MAK17-10-1	South Africa	MV126	09MAK17-25-1	South Africa
MV90	09MAK17-26-1	South Africa	MV127	09MAK9-89	South Africa
MV91	09MAK9-198	South Africa	MV128	09MAK17-35-1	South Africa
MV92	09MAK9-192	South Africa	MV129	09MAK9-127	South Africa
MV93	09MAK7-68	South Africa	MV130	WL429-13	Uganda
MV94	09MAK9-170	South Africa	MV131	WL118-2	Uganda
MV95	09MAK7-3	South Africa	MV132	WL429-14	Uganda
MV96	09MAK17-51-1	South Africa	MV133	WL429-23	Uganda
MV97	09MAK9-155	South Africa	MV134	WL118-10	Uganda

Appendix 3.1: continued

Genotype No.	Pedigree/designation	Origin	Genotype No.	Pedigree/designation	Origin
MV135	WL118-14	Uganda	MV158	WL429-33	Uganda
MV136	WL429-40	Uganda	MV159	WL429-17	Uganda
MV137	WL118-6	Uganda	MV160	WL429-20	Uganda
MV138	WL-118-11	Uganda	MV161	WL429-1	Uganda
MV139	WL118-16	Uganda	MV162	WL429-21	Uganda
MV140	WL118-26	Uganda	MV163	WL118-13	Uganda
MV141	WL429-6	Uganda	MV164	WL429-26	Uganda
MV142	WL-118-3	Uganda	MV165	WL118-12	Uganda
MV143	WL429-19	Uganda	MV166	WL118-11	Uganda
MV144	WL429-12	Uganda	MV167	WL429-18	Uganda
MV145	WL429-16	Uganda	MV168	WL118-7	Uganda
MV146	WL429-38	Uganda	MV169	WL118-8	Uganda
MV147	WL118-22	Uganda	MV170	WL118-9	Uganda
MV148	WL429-41	Uganda	MV171	WL429-36	Uganda
MV149	WL118-1	Uganda	MV172	WL429-39	Uganda
MV150	WL429-34	Uganda	MV173	WL429-5	Uganda
MV151	WL429-30	Uganda	MV174	WL118-19	Uganda
MV152	WL429-8	Uganda	MV175	WL118-15	Uganda
MV153	WL429-25	Uganda	MV176	WL118-17	Uganda
MV154	WL429-27	Uganda	MV177	WL429-35	Uganda
MV155	WL429-15	Uganda	MV178	WL429-24	Uganda
MV156	WL429-43	Uganda	MV179	WL118-4	Uganda
MV157	WL429-37	Uganda	MV180	WL429-31	Uganda

Chapter Four

Diallel analysis of weevil resistance in eastern and southern Africa maize germplasm lines

Abstract

The maize weevil (*Sitophilus zeamais* Motschulsky) is a cosmopolitan insect pest affecting stored maize grain in the tropical and subtropical zones worldwide. Host plant resistance is the cheapest and most sustainable control strategy against weevils. Thus, information on combining ability and gene action conditioning weevil resistance would be required for weevil resistance breeding programs. The current study investigated gene action governing weevil resistance in ten inbred lines. Eight weevil resistant and two susceptible inbred line parents were crossed in a 10 x 10 full diallel mating design. The resulting F₁ hybrid seed, F₂ full-sib and F₂ half-sib grain categories generated directly from the 45 crosses and their reciprocal crosses evaluated for weevil resistance. Response to weevil infestation was determined using F₁ weevil progeny emergence, median development period (MDP), Dobie's index of susceptibility (DIS), and parental weevil mortality. General combining ability (GCA), specific combining ability (SCA) and reciprocal effects were all significant for F₁ weevil progeny emergence, MDP, and DIS in the three seed categories. The GCA effects were not significant for parent weevil mortality. The results revealed that weevil resistance was governed by additive gene action, non-additive, and maternal effects. Parents MV170 and MV142, and hybrids MV75 x MV154, MV154 x MV142, MV142 x MV170, MV154 x MV31, and MV170 x MV13 were consistently exhibiting weevil resistance in the three seed categories and thus recommended for future weevil breeding strategies.

Key words: Combining ability, maize, maize weevil resistance,

4.1 Introduction

The maize weevil (*Sitophilus zeamais* Motschulsky) is one of the most destructive storage pests of maize, prevalent in all maize growing zones worldwide. Losses in grain weight associated with the maize weevil are not well documented in Uganda; however, Ngatia and Kimondo (2011) reported a cumulative grain weight loss of up to 20% under crib conditions and more than 25% under house conditions in Kenya. Weevils not only cause grain weight losses but also lead to quality deterioration, as the infested grain usually acquires an off-odor in addition to paving way for secondary infections by molds especially *Aspergillus* and other ear rot pathogens (Barney et al., 1991; Sone, 2001). Improper grain handling and management through mixing of well-dried and poorly dried grains, mixing old maize batches with new ones are responsible for the survival of the maize weevil from one cropping season to another (Ajibola, 1971; Barney et al., 1991). From the storage facilities, the maize weevil initiates infestation of the new maize crop in the field (Ajibola, 1971; Giles and Ashman, 1971; Demisse et al., 2008). Thus, weevil prevalence both in the field and under storage complicates its control.

Various measures are used to control weevil infestations and ultimately damage of the maize grain. The most commonly used control measure is commercial insecticides. However, the cost implications associated with chemicals especially for small scale farmers, development of insecticide resistance by the maize weevils, and their eco-unfriendliness render chemicals unsustainable (Corrêa et al., 2011). Other weevil control measures tested include use of biological control agents especially *Beauveria* spp. (Adane et al., 1996); and botanical extracts and indigenous technical knowledge (Demissie et al., 2008); but their application is limited to subsistence scale. Accordingly, host plant resistance would provide a cheap, environmentally sound and sustainable alternative weevil control measure. Weevil resistant maize germplasm has been reported and genotypes with enhanced weevil resistance have been developed (Dhliwayo and Pixley, 2003; Dari et al., 2010; Mwololo et al., 2012). However, no weevil resistant maize varieties have been identified and deployed in Uganda, except for the few inbred lines being evaluated for weevil resistance in this study.

Introduction of new sources of weevil resistance from exotic maize germplasm would enhance the development of adapted, weevil resistant maize cultivars. Information on combining ability for yield and weevil resistance, heritability and gene action conditioning weevil resistance would guide breeders in germplasm selection and designing appropriate breeding strategies when breeding for weevil resistance.

Genetic studies are usually conducted on F_1 hybrid seed which is planted by farmers to obtain F_2 grain that is stored for home consumption or for sale. Therefore, it is F_2 grain which is prone to weevil damage and thus requiring adequate resistance. For the purpose of integrating the seed categories usually utilized at research and farmer levels, the study involved determining the genetics of weevil resistance in three categories of maize seed. The first category was the F_1 hybrid seed which was basically parental inbred line seed obtained by crossing with another inbred line parent; the second category was F_2 full-sib seed that was obtained through sib-mating of F_1 hybrids (single crosses) generated by planting F_1 hybrid seed; while the third category was F_2 half-sib seed that was generated by outcrossing F_1 hybrid plants derived from F_1 hybrid seed. Existence of genetic correlation among the three seed categories would be desirable, because it would justify the use of only one seed generation to obtain adequate genetic information.

This would save time and costs involved in conducting more than one study. The objectives of the study were: i) to determine the combining ability and gene action conditioning weevil resistance in the maize germplasm, ii) to identify weevil resistant inbred line parents for future weevil breeding strategies. The knowledge would be used in devising new breeding strategies to obtain grain weevil resistant maize varieties.

4.2 Materials and Methods

4.2.1 Germplasm

The study materials comprised of ten parental lines from the eastern and southern Africa maize germplasm at advanced evaluation stages. Germplasm was acquired from three sources namely: the National Crops Resources Research Institute (NaCRRI), based at Namulonge 30 km north of Kampala, Uganda; the International Maize and Wheat Improvement Center (CIMMYT-Kenya), these contributed the eastern Africa germplasm; while parental lines from the University of KwaZulu Natal, Republic of South Africa constituted germplasm from southern Africa. The germplasm was evaluated for agronomic performance in 2010A at NaCRRI, and subsequently screened for weevil resistance in 2010B in the laboratory at Namulonge. An index was used to select the best three performing inbred lines from each source. The major traits considered in the index also included the attributes that were prioritized by farmers during participatory rural appraisal (PRA) and these were high yields, resistance to field pests and

foliar diseases, early maturity, and weevil resistance (see chapter two). Weevil resistance was scored highly because it was on average ranked among the top four major constraints encountered in maize production in the districts of Kasese, Nakaseke and Kapchworwa where the PRA study had been conducted. Eight weevil resistant and two susceptible inbred lines were used in a 10 x 10 full diallel mating design. The genotype names, their sources and response to weevil infestations are shown in Table 4.1.

Table 4.1: Code names, pedigrees, origin and characteristics of parents used in the 10 x 10 full diallel mating design

Genotype code	Pedigree/parents	Origin	Response to Weevil infestation
MV21	CML507	CIMMYT-Kenya	Resistant
MV154	WL429-27	Uganda	Resistant
MV31	[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-B//EV7992/EV8449...-3-2-2-1-BBBBB-B-B-B	CIMMYT-Kenya	Resistant
MV44	[(CML395/CML444)-B-4-1-3-1-B/CML444//[[TUXPSEQ]C1F2/MV449-SR]F2-45-7-1-2-BBB]-2-1-2-2-BBB-B-B-B	CIMMYT-Kenya	Susceptible
MV13	CKL05019	CIMMYT-Kenya	Resistant
MV63	09MAK17-15-1	South Africa	Resistant
MV75	09MAK17-28-1	South Africa	Resistant
MV102	09MAK9-157	South Africa	Susceptible
MV170	WL118-9	Uganda	Resistant
MV142	WL-118-3	Uganda	Resistant
Check 1	Longe5 (OPV)	Uganda	Susceptible
Check 2	Genotype # 10 [weevil/CML312]-B-13-2-1-BBB/[weevil/CML387]-B-9-1-1 (inbred)	CIMMYT-Zimbabwe	Resistant
Check 3	Genotype # 11 07WEEVIL (inbred)	CIMMYT-Zimbabwe	Resistant
Check 4	Longe10H (hybrid)	Uganda	Susceptible
Check 5	Popcorn (local OPV)	Uganda	Susceptible
Check 6	Longe6H (hybrid)	Uganda	Susceptible
Check 7	CML312/CML442 (Heterotic group A tester -hybrid)	CIMMYT-Kenya	Susceptible
Check 8	CML202/CML395 (Heterotic group B tester-hybrid)	CIMMYT-Kenya	Susceptible

The nurseries were planted in March, 2011A season at NaCRRI, Namulonge (1200 m.a.s.l); 0°32'N, 32°34'E; 1300 mm bimodal rainfall. The row length was 5 m with an inter row spacing of 0.75 m, while the intra row spacing was 0.3 m. Twenty rows of each inbred line parent were planted in an alternating arrangement, in such a way that each line had an equal chance of being crossed with the remaining parental lines. To provide for cultivar differences in flowering periods, three staggered plantings of each inbred line were made at intervals of five days between each planting. This improved synchronization of silking and pollen shedding among the parental lines.

4.2.2 Seed harvesting and preparation

At physiological maturity, the cobs were harvested, labeled, and ears from the main crosses were bulked differently from the reciprocal crosses. The ears were then dried, after which they were shelled. A total of 100 genotypes comprising of 90 experimental hybrids and ten parental lines were shelled and ultimately evaluated for field performance and response to weevil infestations. Therefore, two seed batches were obtained. The first batch was prepared for trial establishment under two environments, while the second batch was prepared for screening against weevils. Remnant seed was kept for each genotype.

4.2.3 Field evaluations

The 90 experimental hybrids obtained from the 10 x 10 full diallel were evaluated along with the ten parental lines. The ten inbred line parents were planted in a separate trial nearby, to avoid competition with the taller hybrids. The trial was established at the National Crops Resources Research Institute (NaCRRI), Namulonge (0°32'N, 32°34'E, 1200 m.a.s.l.), for two seasons, in 2011B and 2012A. The field trial for the experimental hybrids was arranged in a 10 x 9 alpha lattice design with two replications; while the one for the parents was a randomized complete block design, with two replications. Two row plots of length 5 m, inter-row spacing 0.75 m, and intra-row spacing 0.30 m, were planted, giving a plant population of 44,444 plants per hectare. Di-ammonium phosphate (18% P) was applied at a rate of 120 kg P ha⁻¹, at planting; while urea (46% N) was applied at a rate of 120 kg N ha⁻¹, 21 days after planting.

For comparison of the influence of full-sib mating and half-sib mating on gene action and combining ability for weevil resistance, at least five plants in the second row of each plot, were sib-mated. Sib-mating (generation of F₂ full-sib) was achieved by collecting pollen from within each row bulking it, and pollinating plants with receptive silks within each row. The silks and tassels of the sib-mated plants were protected from contamination with unwanted pollen, using shoot bags and tassel bags, respectively. The rest of the plants were left to outcross, and as a result generated F₂ half-sib grain.

4.2.4 Field data collection

Data were collected on a number of parameters including: period to anthesis and silking, plant and ear heights, the number of ears per plant, ear aspect and grain texture. However, for

purposes of this study, only results on grain texture and yield are reported. The plants were harvested at dry maturity and genotype field weight estimated. The ears were scored for grain texture using a scale of 1 to 5, where: 1 = ears with 100% shiny-flint kernels; 2 = ears with flint kernels mixed with semi-flint and semi-dent kernels; 3 = ears with the same proportion of semi-flint and semi-dent kernels; 4 = ears with semi-dent kernels mixed with dent kernels; and 5 = ears with over 75% dent kernels. Finally ears were sampled to obtain grain for estimation of moisture content (%). All ears from each plot were then weighed to establish their field weight (kg plot⁻¹), after which they were dried, shelled, and grain prepared for screening against the maize weevil in the laboratory.

4.2.5 Weevil culture rearing

Weevil culture rearing and grain testing for weevil resistance was conducted as described in Chapter Three (Section 3.2.5).

4.2.6 Data collected on weevil parameters

Data were recorded on the number of parental weevils alive and dead (recorded at parents' removal); F₁ weevil progenies emerging every two days (F₁ weevils alive and dead), this was done until no more F₁ weevils were emerging and the total was determined; the median development period (MDP), was calculated as the period in days, from the middle of the oviposition period to the emergence of 50% of the F₁ weevil progenies (Dobie, 1977). Dobie's index of susceptibility was calculated based on total F₁ weevil emergence and the median development period (Dobie, 1974). It was calculated using the formula:

$$\text{DIS} = \frac{\text{In F1 weevil progeny emergence}}{\text{Median Development Period}} \times 100$$

4.2.7 Data analysis

Data were analysed using SAS version 9.1 procedure general linear models (SAS-Institute, 2003). The genetic information of the parameters was obtained by subjecting the data to Griffing's method 1 model 1 (Griffing, 1956). Estimation of general combining ability (GCA), specific combining ability (SCA), and reciprocal effects (REC), and the partitioning of reciprocal effects into maternal (MAT) and non-maternal effects (NMAT) of the 10 parental lines, was done

using diallel SAS05 program (Zhang et al., 2005) in SAS. The genotypes were considered as fixed effects, while the environments and replications within environments were considered as random effects.

The model used in the analysis was: $Y_{ijkl} = \mu + g_i + g_j + r_{ij} + s_{ij} + \frac{1}{bc} \sum_k \sum_l e_{ijkl}$

Y_{ijkl} = observed measurement for the ij^{th} cross in the k^{th} replication, under the l^{th} environment combination, μ = is the population mean; g_i and g_j = General combining ability (GCA) effects for the i^{th} and j^{th} parental lines, respectively; r = reciprocal effects, such that $r_{ij} = -r_{ji}$; s_{ij} = Specific combining ability (SCA) effect for the ij^{th} cross; and e_{ijkl} = error term associated with the ij^{th} cross evaluated in the k^{th} replication under the l^{th} environment combination.

The relative significance of the GCA and SCA effects was determined, based on the proportion of one of the two factors to the total genetic effects, as described by Baker (1978). Thus, the proportion of GCA was calculated as: $2\sigma_{\text{GCA}}^2 / (2\sigma_{\text{GCA}}^2 + \sigma_{\text{SCA}}^2)$. The closer the ratio is to unity the more important GCA would be in predicting progeny performance (Baker, 1978). Additionally, the significance of maternal and non-maternal effects as proportions of the reciprocal cross effects was also determined.

4.2.8 Estimation of narrow sense heritability

The narrow sense heritability (h^2) estimates for weevil resistance as exhibited by the number of F_1 weevil progenies emerging from F_1 hybrid seed, F_2 full-sib and F_2 half-sib seed of the 90 experimental hybrids were estimated as regressions of the mean F_1 weevils emerging from the experimental hybrids against the mid-parent values as described by Smalley et al. (2004).

4.3 Results

4.3.1 F_1 hybrid seed assessment

4.3.1.1 Genetic variation

The mean squares for F_1 weevil progeny emergence, median development period (MDP), Dobie's Index of susceptibility (DIS), and parental weevil mortality in the F_1 hybrid seed are shown in Table 4.2. The mean squares for F_1 weevil progenies that emerged from the F_1 seed

indicated that all the main effects namely genotype, general combining ability (GCA), specific combining ability (SCA), reciprocal effects (REC), maternal (MAT), non-maternal effects (NMAT) were highly significant ($P < 0.001$). The mean number of F_1 weevil progenies that emerged was 17 weevils. Regarding the importance of the genetic effects towards the governance of F_1 weevil progeny emergence, reciprocal effects contributed 47.0%, SCA effects constituted 31.0%, whereas GCA effects constituted 22.0% of the genotype sum of squares.

The mean squares for the median development period (MDP) indicated that all main effects were significant ($P < 0.05$ – $P < 0.001$). The mean median development period was 43.2 days. As regards to the influence of the genetic components towards the governance of the median development period, the GCA effects were contributing 41.3%, the SCA effects were contributing 22.0%, while the reciprocal effects were contributing 36.7% of the genotype sum of squares for the median development period.

Means squares for Dobie index of susceptibility (DIS), revealed that all effects including genotype, GCA, SCA, MAT and NMAT effects were highly significant ($P < 0.001$). The reciprocal effects constituted the largest proportion of the genotype sum of squares amounting to 53%; this was followed by the SCA effects which constituted 27%, whereas the GCA effects constituted 20% of the genotype sum of squares. Similarly, for parental weevil mortality, the mean squares indicated that all main effects were highly significant ($P < 0.001$); the reciprocal effects constituted 50.6% of the genotype sum of squares, SCA effects constituted 25.1%, while GCA constituted 24.3%. The mean parental weevil mortality was 16 weevils.

Regarding hybrid response to weevil attack, vivid variations were observed between the main and reciprocal crosses for a number of crosses. An example for the response of F_1 hybrid seed generated from crosses between resistant and susceptible parental lines is presented in Figure 4.1a. When a susceptible line, MV21, was used as a female parent in the cross MV21 x MV142, the resulting hybrid seed was susceptible to weevil attack. However, the hybrid seed that was generated by the reciprocal cross (MV142 X MV21) was resistant to weevil attack. On the other hand, the hybrid seed generated from both main and reciprocal crosses between susceptible parental lines (e.g. MV21 and MV63) was susceptible to weevil attack (Figure 4.1b).



a.



b.

Figure 4. 1: Response of experimental hybrids to weevil attack. a: between susceptible and resistant parental lines; b: between susceptible and susceptible lines.

Table 4.2: Mean square for F₁ weevil progeny emergence, median development period, Dobie index of susceptibility, parental and F₁ weevil mortality in the F₁ hybrid seed of the study genotypes at Namulonge in seasons 2011A and B

Source	DF	Mean Squares			
		FWE	MDP	DIS	PWM
REP	2	413.17	10.33	70.73	99.02
GENOTYPE	99	254.27***	68.47***	14.01***	159.61***
GCA	9	613.85***	310.83***	65.29***	426.14***
SCA	45	173.55***	33.12*	17.66***	88.18***
REC	45	263.07***	55.34***	34.53***	177.73***
MAT	9	605.56***	154.42***	71.36***	414.62***
NMAT	36	177.45***	30.58*	25.32***	118.51***
R ²		0.63	0.63	0.62	0.76
CV (%)		53.08	10.42	32.00	30.70
Hybrid mean		16.54	43.15	5.86	16.28
GCAss (%)		21.95	41.27	0.20	24.27
SCAss (%)		31.02	21.99	0.27	25.11
RECss (%)		47.03	36.74	0.53	50.61

*, **, *** indicate the value is significant at P≤0.05, P≤0.01 and P≤0.001, respectively; FWE = F₁ weevils emerged, MDP = median development period, DIS = Dobie's index of susceptibility, PWM = parent weevil mortality.

4.3.1.2 General combining ability estimates

Results for the general combining ability effects for weevil resistance in the ten parental lines are presented in Table 4.3. For GCA estimates of the F₁ weevils emerged, parents MV44 and MV102 displayed positive and highly significant (P<0.01 - P<0.001) GCA effects, while parents MV170 and MV142 displayed negative and highly significant (P<0.01) GCA effects. For MDP, parents MV21, MV154, MV31, MV170 and MV142 exhibited positive significant GCA effects, whilst parents MV44, MV63, MV75 and MV102 exhibited negative and highly significant (P<0.01) GCA effects. Parent MV44 exhibited positive highly significant GCA effects for DIS while Parent MV21 exhibited negative significant (P<0.05) GCA effects. Parents MV63, MV170, and MV142 displayed positive significant (P<0.05 – P<0.001) GCA effects for parental weevil mortality, whereas parents MV31 and MV44 displayed negative significant (P<0.05 and P<0.001) GCA effects.

Table 4.3: General combining ability effects for F₁ weevil emergence, median development period, Dobie index of susceptibility, and weevil mortality exhibited in the ten parental lines under F₁ hybrid seed

Parent	FWE	MDP	DIS	PWM
MV21	0.53	1.17*	-0.77*	-0.68
MV154	-1.87	1.43**	-0.63	0.09
MV31	0.91	2.15***	-0.43	-1.49*
MV44	6.93***	-3.62***	1.27***	-5.69***
MV13	0.46	-0.70	-0.03	-1.16
MV63	-1.11	-1.73**	0.46	1.37*
MV75	-1.56	-1.47**	0.18	0.99
MV102	2.96**	-2.42***	0.52	-0.23
MV170	-4.17**	3.13***	-0.23	4.5***
MV142	-3.07**	2.05***	-0.35	2.11***
Standard	±1.10	±0.55	±0.36	± 0.62
Errors				

*, **, *** indicate the value is significant at P≤0.05, P≤0.01 and P≤0.001, respectively; FWE = F₁ weevils emerged, MDP = median development period, DIS = Dobie's index of susceptibility, PWM = parent weevil mortality.

4.3.1.3 Specific combining ability effects

Results of the SCA estimates for weevil resistance in 45 main crosses and 45 reciprocal crosses, manifested as F₁ weevil emergence are presented in Table 4.4. The results indicated that two main crosses MV75 x MV21 and MV75 x MV13 exhibited negative and significant (P<0.05) SCA effects, whereas their reciprocal crosses MV21 x MV75 and MV13 x MV75 exhibited positive non-significant SCA effects. Two other main crosses, MV44 x MV63 and MV44 X MV75, displayed positive significant SCA effects, while their reciprocal crosses MV63 x MV44 and MV75 x MV44 displayed negative but not significant SCA effects. For parental lines MV170 and MV31, both main cross MV170 X MV31 and reciprocal cross MV31 x MV170 exhibited positive and significant SCA effects. Most of the crosses involving susceptible parents MV44 and MV102 as female parents displayed positive SCA effects, whereas most of the crosses involving resistant parents MV170 and MV142 displayed negative SCA effects.

Table 4.4: Specific combining ability estimates for weevil resistance manifested by F₁ weevil progenies that emerged from F₁ hybrid seed of the 45 crosses and their reciprocals

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		4.47	-3.48	-2.83	-0.53	-0.13	-6.51*	2.64	-1.73	5.27
MV154	7.00		-4.08	3.24	-5.13	0.12	3.56	-3.29	-3.66	-7.63
MV31	6.50	1.50		0.79	7.42*	-1.51	-3.89	-9.24**	14.89***	2.48
MV44	-3.83	1.83	-7.83*		4.24	-3.36	-0.91	1.24	4.87	-6.83
MV13	10.33**	2.67	3.33	9.17		0.77	-9.67**	-3.29	0.17	1.70
MV63	-2.50	8.67*	2.17	10.67**	1.33		0.46	5.11	-3.26	-0.87
MV75	0.33	6.33	-1.00	7.67*	2.89	-0.67		-8.61*	-3.98	-21.48***
MV102	-11.00**	-3.67	-2.83	1.33	-0.67	-6.83	1.00		-5.83	-17.80**
MV170	5.50	0.83	19.83***	2.83	4.00	3.67	-0.50	5.50		2.23
MV142	14.67***	-0.50	-6.50	5.83	-1.17	-2.17	4.67	13.83***	-0.33	

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively

For DIS, the results indicated that crosses MV154 x MV21, MV31 x MV21, MV142 x MV21, MV13 x MV44, MV170 x MV31 and MV142 x MV102 exhibited positive significant ($P < 0.05$ – $P < 0.001$) SCA effects, whereas crosses MV44 x MV21, MV75 x MV21, MV102 x MV154, MV44 x MV31, MV75 x MV31, and MV142 x MV170 exhibited negative significant ($P < 0.05$ – $P < 0.01$) SCA effects (Appendix 4.2).

As regards to parental weevil mortality (Appendix 4.3), the results indicated that crosses MV44 x MV13, MV13 x MV63, MV102 x MV21, MV31 x MV75, MV102 x MV142 and MV154 x MV63 exhibited negative significant ($P < 0.05$ – $P < 0.001$) SCA estimates, while their reciprocal crosses (MV13 x MV44, MV63 x MV13, MV21 x MV102, MV75 x MV31, MV142 x MV102 and MV63 x MV154) exhibited positive significant SCA effects. For other crosses such as MV142 x MV170 and MV13 x MV21, positive significant SCA effects were manifested in both main and reciprocal crosses.

4.3.2 F₂ full-sib grain assessment

4.3.2.1 Genetic variation

Mean squares for F₁ weevil progeny emergence, median development period (MDP), Dobie' Index of susceptibility (DIS), and parental weevil mortality in the F₂ full-sib grain obtained from

the 90 crosses of the 10 x 10 full diallel mating are shown in Table 4.5. The mean squares for F_1 weevil progenies that emerged from the F_2 full-sib grain indicated that all the main effects namely environment (ENV), genotype, general combining ability (GCA), specific combining ability (SCA), reciprocal effects (REC), maternal (MAT), non-maternal effects (NMAT) were significant ($P < 0.05$ – $P < 0.001$). All the interactions between the main effects and the environment were also significant ($P < 0.05$ – $P < 0.001$). The mean number of F_1 weevil progenies that emerged was 44.3 weevils. Regarding the importance of the genetic effects towards weevil resistance, GCA constituted the highest proportion of 67.6% to the genotype sum of squares, followed by SCA with 21.6%, while the reciprocals contributed 10.8%.

The mean squares for the median development period (MDP) indicated that all main effects were highly significant ($P < 0.001$), except for maternal effects that were significant at 5% probability level ($P < 0.05$). The interactions between GCA and environment, and SCA and environment were not significant ($P > 0.05$), while the remaining interactions between genotype and environment, reciprocal effects and environment, maternal effects and environment, and non-maternal effects and environment were highly significant ($0.01 > P < 0.001$). For Dobie's index of susceptibility (DIS), all the main effects were significant ($P < 0.05$ – $P < 0.001$); similarly, all interactions that is, GCA x environment, genotype x environment, reciprocal effects x environment, maternal effects x environment, SCA x environment, and non-maternal effects x environment were significant ($P < 0.05$ – $P < 0.001$). As regards to the overall significance of the genetic effects, the GCA effects were contributing 57.9% and 67.4%, SCA effects were contributing 29.8% and 24.2%, while reciprocal effects were contributing 14.0% and 8.4% of the genotype sum of squares for MDP and DIS, respectively.

For weevil parental mortality, all the main effects namely genotype, GCA, SCA, reciprocal effects, maternal and non-maternal effects were highly significant ($P < 0.01$ – $P < 0.001$); for the interactions, GCA x environment interaction was significant ($P < 0.05$), while the rest of the interactions were not significant ($P > 0.05$). The mean parental mortality was 9.2 weevils. As regards to the significance of the genetic effects, the reciprocal effects were contributing 45%, SCA effects were contributing 38.5%, while GCA effects were contributing 16.2% of the genotype sum of squares.

Table 4.5: Mean square for F₁ weevil progeny emergence, median development period, Dobie index of susceptibility, parental and F₁ weevil mortality in the parental lines and F₂ full-sib grain

Source	DF	Mean Squares			
		FWE	MDP	DIS	PWM
ENV	1	82052.33***	1022.00***	463.77***	8.07
REP(ENV)	4	7572.90	313.30	63.51	499.01
GENOTYPE	99	1792.57***	32.53***	13.74***	53.73***
GCA	9	13812.74***	215.69***	106.50***	95.63***
SCA	45	884.48***	21.33***	7.66***	45.48***
REC	45	432.66***	10.04***	2.66***	53.51***
MAT	9	404.42*	10.73*	2.32*	129.67***
NMAT	36	439.72***	9.87***	2.74***	34.47**
ENV*GENOTYPE	99	359.40***	6.69**	2.04***	18.71
GCA*ENV	9	572.67***	5.81	2.51**	40.36*
SCA*ENV	45	295.75**	6.04	1.70**	16.83
REC*ENV	45	380.73***	8.34***	2.38***	15.37
MAT*ENV	9	713.05***	11.39**	5.17***	19.51
NMAT*ENV	36	297.65*	7.57**	1.68**	14.34
R ²		0.82	0.78	0.86	0.55
CV (%)		30.11	4.52	12.58	46.53
Hybrid mean		44.33	46.64	7.77	9.22
GCAss (%)		67.60	57.90	67.37	16.19
SCAss (%)		21.60	29.81	24.23	38.51
RECss (%)		10.80	14.03	8.40	45.30

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively; FWE = F₁ weevils emerged, MDP = median development period, DIS = Dobie's index of susceptibility, PWM = parent weevil mortality.

4.3.2.2 General combining ability estimates

The general combining ability effects for weevil resistance in the ten parental lines, exhibited in F₁ weevil progeny emergence, median development period, Dobie's index of susceptibility, and parental weevil mortality are presented in Table 4.6. The GCA estimates for F₁ weevil

emergence, showed that parents MV44 and MV102 displayed positive and highly significant ($P < 0.001$) GCA effects, which in this case is undesirable as it indicates an increase in F_1 weevil progeny emergence. On the other hand, parents MV21, MV154, MV170, and MV142 displayed negative and highly significant ($P < 0.01 - P < 0.001$) GCA effects. For MDP, parents MV154, MV31, MV170, and MV142 exhibited positive significant GCA effects, whilst parents MV44, and MV102 exhibited negative and highly significant ($P < 0.001$) GCA effects. For DIS, parents MV44, MV75, and MV102 exhibited positive significant ($P < 0.05 - P < 0.001$) GCA effects, while parents MV21, MV154, MV31, MV170, and MV142 exhibited negative significant ($P < 0.01 - P < 0.001$) GCA effects. For parental weevil mortality, parent MV21 displayed positive significant ($P < 0.01$) GCA effects, whereas parents MV31, MV44 and MV102 displayed negative highly significant ($P < 0.01$) GCA effects.

Table 4.6: General combining ability estimates for weevil resistance displayed in the ten parental lines as exhibited by F_1 weevil emergency from F_2 full-sib seed

Parent	FWE	MDP	DIS	PWM
MV21	-5.75**	0.07	-0.33*	1.31**
MV154	-4.96**	0.57*	-0.28*	-0.18
MV31	-2.42	0.63*	-0.38**	-1.11**
MV44	14.14***	-2.02***	1.27***	-1.11**
MV13	1.25	0.17	0.15	0.76
MV63	2.34	-0.02	0.25	-0.01
MV75	4.28*	0.03	0.34*	0.53
MV102	18.40***	-2.45***	1.51***	-1.23**
MV170	-17.91***	2.13***	-1.69***	0.71
MV142	-9.38***	0.90***	-0.84***	0.33
Standard Errors	±1.78	±0.26	±0.13	± 0.41

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively; FWE = F_1 weevils emerged, MDP = median development period, DIS = Dobie's index of susceptibility, PWM = parent weevil mortality.

4.3.2.3 Specific combining ability effects

Specific combining ability effects data for weevil resistance as manifested by F_1 weevil progeny emergence from F_2 full-sib grain are presented in Table 4.7. The results showed two main crosses (MV142 x MV44 and MV170 x MV31), exhibiting negative and significant SCA effects.

Their reciprocal crosses (MV44 x MV142 and MV31 x MV170) on the other hand, exhibited negative but not significant SCA effects. Conversely, crosses MV142 x MV31, MV170 x MV21, and MV21 x MV13 exhibited positive significant SCA effects, while their reciprocal crosses (MV31 x MV142, MV21 x MV170, and MV13 x MV21) displayed positive but not significant SCA effects. Only cross MV170 x MV44 exhibited negative and significant SCA effects, that were in the opposite direction to that of their reciprocal cross (MV44 x MV170), which was positive but not significant ($P>0.05$).

Table 4.7: Specific combining ability resistance manifested by F_1 weevil progenies that emerged from F_2 full-sib seed generated from the 45 crosses and their reciprocals

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		6.71	4.00	1.03	2.25	4.41	-0.69	-0.65	10.49*	3.13
MV154	-6.00		1.13	-1.27	0.54	-3.30	-3.98	-5.11	-1.13	-5.42
MV31	-16.50**	2.41		-6.06	-4.25	-8.93	5.39	6.85	-18.59***	20.13*
MV44	-5.42	1.08	5.83		-2.56	-8.65	0.33	-1.21	-14.98**	-43.73***
MV13	12.25**	75.00	0.58	6.67		-7.84	-5.44	-1.07	10.65*	0.04
MV63	1.67	-3.92	-8.33	-2.33	5.92		-0.87	5.59	9.40	-8.45
MV75	-9.00	-4.50	-0.58	-1.58	-8.42	-1.92		-4.18	-0.53	13.07
MV102	-7.17	5.33	-7.00	-0.33	8.25	-6.67	-3.67		5.18	-1.48
MV170	9.33	7.50	-0.58	0.25	-4.17	-3.33	9.83	0.00		2.22
MV142	9.50	-2.33	1.00	-1.92	2.08	-3.50	1.08	0.92	-6.58	

*, **, *** indicate the value is significant at $P\leq 0.05$, $P\leq 0.01$ and $P\leq 0.001$, respectively

Results of the SCA effects for the median development period, Dobie's index of susceptibility, and parental weevil mortality manifested in F_2 full-sib grain are shown in appendices 4.4, 4.5, and 4.6, respectively. The specific combining ability effects data (Appendix 4.4) for the MDP of F_1 weevil progenies that emerged from F_2 full-sib grain, indicated that both the main cross MV142 x MV44, and reciprocal cross MV44 x MV142, exhibited positive and significant SCA effects. Three main crosses MV170 x MV154, MV170 x MV44 and MV44 x MV31 exhibited positive and significant SCA effects, while their reciprocal crosses (MV154 x MV170, MV44 x MV170, and MV31 x MV170) exhibited negative and non-significant SCA effects.

For the DIS, main crosses MV142 x MV44 and MV170 x MV31, exhibited negative and significant SCA effects, while their reciprocal crosses MV44 x MV142 and MV31 x MV170 displayed negative non-significant SCA effects. Cross MV170 x MV44 exhibited negative significant SCA effects, while its reciprocal cross MV44 x MV170 exhibited positive non-

significant SCA effects. Main cross MV142 x MV21 exhibited negative non-significant SCA effects, whereas its reciprocal cross MV21 x MV142 exhibited positive significant SCA effects. Cross MV102 x MV170, exhibited positive significant SCA effects, whereas its reciprocal cross MV170 x MV102 displayed positive non-significant SCA effects (Appendix 4.5).

As regards to parental weevil mortality, cross MV142 x MV75 exhibited negative and highly significant ($P < 0.001$) SCA effects, while its reciprocal MV75 x MV142 displayed negative but non-significant SCA effects. Cross MV170 x MV21 displayed positive significant SCA effects and its reciprocal displayed positive but non-significant SCA effects. Crosses MV63 x MV154 displayed positive significant SCA effects, while its reciprocal MV154 x MV63 displayed negative non-significant SCA effects. On the other hand, cross MV44 x MV170 that was negative and significant, its reciprocal cross exhibited positive non-significant SCA effects (Appendix 4.6).

4.3.3 F₂ half-sib grain assessment

4.3.3.1 Genetic variation

Means squares for F₁ weevil emergence, median development period, Dobie's index of susceptibility, and parental weevil mortality in the ten parental lines and F₂ half-sib grain of the 45 experimental hybrids are shown in Table 4.8. Mean squares for F₁ weevil progenies that emerged from the F₂ half-sib seed indicated that all main effects: environment (ENV), genotype, general combining ability (GCA), specific combining ability (SCA), reciprocal effects (REC), maternal (MAT), non-maternal effects (NMAT) were highly significant ($P < 0.001$). All the interactions between the main effects and the environment were also significant ($P < 0.05$ – $P < 0.001$). As regards to the importance of the genetic effects towards weevil resistance, SCA effects constituted the highest proportion of 40.4% to the genotype sum of squares, followed by reciprocal effects with 32.2%, while GCA effects contributed 27.4%.

Table 4.8: Mean squares for F₁ weevil progeny emergence, median development period, Dobie' index of susceptibility, parent weevil mortality in the F₂ half-sib

Source	DF	Mean square			
		FWE	MDP	DIS	PWM
ENV	1	6428.80***	2.41	38.52***	7.26
REP(ENV)	4	645.49**	2.45	4.70***	15.78
GENOTYPE	99	1442.04***	107.44***	16.03***	32.13*
GCA	9	4350.95***	280.10***	50.32***	34.14
SCA	45	1281.29***	130.09***	17.53***	42.50**
REC	45	1021.01***	50.09***	7.68***	21.37
MAT	9	2701.34***	211.28***	28.08***	16.52
NMAT	36	600.93***	9.80***	2.58***	22.58
ENV*GENOTYPE	99	433.19***	5.90	1.58***	34.62**
GCA*ENV	9	1810.63***	3.94	5.55***	28.01
SCA*ENV	45	305.46***	4.98	1.11*	31.38
REC*ENV	45	285.43***	7.32*	1.26**	39.19**
MAT*ENV	9	273.25*	12.96**	1.55*	23.28
NMAT*ENV	36	288.47***	5.91	1.19*	43.17**
R ²		0.77	0.85	0.86	0.41
CV (%)		33.32	4.93	10.97	52.0
Hybrid mean		36.14	44.48	7.87	9.30
GCAss (%)		27.43	23.78	28.53	9.66
SCAss (%)		40.39	55.03	49.69	60.12
RECss (%)		32.18	21.19	21.78	30.22

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively; FWE = F₁ weevils emerged, MDP = median development period, DIS = Dobie's index of susceptibility, PWM = parent weevil mortality.

The mean squares for median development period (MDP) indicated that genotypes, GCA, SCA, reciprocals, maternal effects and non-maternal effects were highly significant ($P < 0.001$). For the interactions, only reciprocal x environment and maternal effects x environment were significant ($P < 0.05$ – $P < 0.01$). The interactions between genotype x environment, GCA x environment, SCA x environment, and non-maternal effects x environment were not significant ($P > 0.05$). Regarding the significance of the genetic effects towards the governance of the MDP,

GCA effects constituted 23.8% of the genotype sum of squares, SCA contributed 55.0%, while reciprocal effects contributed 21.2%. The mean median development period was 44.5 days.

Regarding Dobie's index of susceptibility (DIS), all the main effects and interactions were significant ($P < 0.05$ – $P < 0.001$). As regards to the overall significance of the genetic effects, the GCA effects contributed 28.5%; SCA effects contributed 49.7%, while reciprocal effects contributed 21.8%. The mean DIS value was 7.9.

For parental weevil mortality, only genotype and SCA mean squares were significant ($P < 0.05$); the remaining main effects (including GCA effects) were not significant ($P > 0.05$). For the interactions, only environment x genotype and reciprocal effects x environment and non-maternal effects x environment were significant ($P < 0.05$ – $P < 0.01$). The remaining interactions were not significant ($P > 0.05$). Regarding the importance of the genetic effects, GCA effects contributed 9.7% of the genotype sum of squares; SCA effects contributed 60.1%, while reciprocal effects contributed 30.2%. Mean parental mortality was 9.3 weevils.

4.3.3.2 General combining ability estimates

Results for the GCA estimates exhibited as resistance to F_1 weevil progeny emergence from the ten parental line seed and the F_2 grain obtained from 45 experimental hybrids and their 45 reciprocal crosses through half-sib mating (out-crossing) at NaCRRI in 2011B and 2012A are shown in Table 4.9. The results showed that parents MV21, MV170 and MV142 displayed negative and significant ($P < 0.05$) GCA estimates. On the other hand, parents MV44 and MV102 manifested positive highly significant ($P < 0.001$) GCA estimates. The rest of the parents did not display significant ($P > 0.05$) GCA estimates as regards to the response to F_1 weevil progeny emergence.

Table 4.9: General combining ability estimates for the ten parents as exhibited by F₁ weevil progeny emergency from F₂ half-sib seed

Parent	FWE	MDP	DIS	PWM
MV21	-3.00*	1.92***	-0.45***	-0.11*
MV154	1.38	0.94***	-0.00	-0.02
MV31	-2.09	0.68***	-0.23**	0.00
MV44	9.52***	-0.09	0.54**	-0.03
MV13	0.77	-0.24	0.14	0.08
MV63	0.15	-0.62**	0.20*	0.12*
MV75	1.73	-1.97***	0.53***	-0.02
MV102	8.38***	-2.95***	1.09***	-0.07
MV170	-9.96***	0.76***	-1.02***	0.01
MV142	-6.88***	1.56***	-0.81***	0.04
Standard Errors	±1.28	±0.19	±0.09	±0.05

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively; FWE = F₁ weevils emerged, MDP = median development period, DIS = Dobie's index of susceptibility, PWM = parent weevil mortality.

For MDP, parents MV21, MV154, MV31, MV170 and MV142 exhibited positive and highly significant ($P < 0.001$) GCA estimates, while parents MV63, MV75, and MV102 exhibited negative highly significant ($P < 0.01 - P < 0.001$) GCA estimates. For DIS, parents MV44, MV63, MV75, and MV102 exhibited positive significant ($P < 0.05 - P < 0.001$) GCA estimates, while parents MV21, MV31, MV170 and MV142 exhibited negative and highly significant ($P < 0.01 - P < 0.001$) GCA effects. For parental mortality, only parent MV63 exhibited positive significant ($P < 0.05$) GCA estimates, while parent MV21 exhibited negative significant ($P < 0.05$) GCA estimates.

4.3.3.3 Specific combining ability effects

The SCA estimates exhibited as resistance against F₁ weevil progeny emergence from F₂ hybrid seed generated through half-sib mating (out-crossing) of 45 experimental hybrids and their 45 reciprocal are shown in Table 4.10. The results showed that main crosses MV142 x MV31, MV142 x MV44, MV142 x MV13 and MV170 x MV44, exhibited negative significant ($P < 0.05 - P < 0.001$) SCA effects, whereas their reciprocal crosses exhibited positive significant ($P < 0.05 -$

P<0.001) SCA effects. For crosses MV170 x MV13 and MV170 x MV102 both the main crosses, and the reciprocal crosses (MV13 x MV170 and MV102 x MV170), exhibited positive and significant SCA effects.

Table 4.10: Specific combining ability estimates for weevil resistance manifested by F₁ weevil progenies that emerged from the 45 hybrids and 45 reciprocal crosses

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		-6.18	3.29	-0.24	0.35	-3.15	-0.61	-0.43	-0.42	-13.71*
MV154	-7.00		-6.01	-1.96	-6.29	-10.66**	6.67	-11.15**	1.70	-17.99*
MV31	-11.00*	7.58		-5.16	5.85	-10.61**	-0.03	-4.60	-4.51	-21.96**
MV44	-18.92***	-9.25*	-1.92		-6.10	-5.56	-7.56*	-4.62	-12.20**	-36.93***
MV13	-0.92	-0.67	-1.67	5.00		-8.72*	-18.39***	-8.87*	10.64**	-29.43***
MV63	-0.50	2.33	1.75	-1.92	-1.00		0.57	14.09***	-1.24	-26.23***
MV75	-7.92	-16.75***	5.58	4.50	-2.25	6.75		-4.00	-5.32	-14.81*
MV102	-3.75	0.92	-14.33***	-4.25	5.42	-5.25	-8.42*		17.78***	-12.08
MV170	5.08	6.92	-4.58	11.00*	8.92*	5.75	3.75	30.50***		-4.67
MV142	-2.08	-4.25	13.08**	21.83***	15.25***	0.08	7.25	8.50*	-0.25	

*, **, *** indicate the value is significant at P≤0.05, P≤0.01 and P≤0.001, respectively.

The SCA estimates for MDP, DIS, and parental mortality are shown in the Appendices 4.7, 4.8, and 4.9, respectively. The MDP for the F₁ weevil progenies that emerged from the F₁ hybrid seed indicated that main crosses MV142 x MV75, MV142 x MV102, MV170 x MV31, MV170 x MV63, MV170 x MV75 exhibited positive and significant SCA effects, while their reciprocals exhibited negative and significant SCA effects. Other main crosses MV142 x MV44, MV142 x MV13 and MV142 x MV63 displayed positive significant SCA effects, whereas their reciprocals displayed negative but not significant SCA effects. All main crosses in which MV142 was used as a female parent exhibited positive and highly significant (P<0.001) SCA effects whereas in its reciprocal crosses, where it served as a female, most of the SCA effects were negative (Appendix 4.7).

The specific combining ability estimates for DIS followed the same trend as those for MDP, but with opposite signs. All types of associations were exhibited between the main and reciprocal crosses for the DIS. For example, main crosses MV142 x MV31, MV142 x MV44, MV142 x MV13, MV142 x MV75, MV142 x MV102, MV170 x MV44, and MV170 x MV75 exhibited negative and significant SCA effects, while their reciprocal crosses exhibited positive and significant SCA effects. Main crosses MV170 x MV102 and MV170 x MV13, and their reciprocal

crosses MV102 x MV170 and MV13 x MV170 exhibited positive significant SCA effects; while main crosses MV102 x MV31 and MV154 x MV21, and their reciprocal crosses MV31 x MV102 and MV21 x MV154 displayed negative and highly significant ($P < 0.01$) SCA effects. For parental weevil mortality, main cross MV102 x MV44 and reciprocal cross MV44 x MV102 both exhibited positive significant SCA effects; both parents MV102 and MV44 exhibited characteristics for susceptible parents. Cross MV102 x MV63 and its reciprocal both exhibited positive SCA effects though the main cross was significant as opposed to the insignificant reciprocal cross. Crosses MV142 x MV75 and MV142 x MV44 exhibited negative and significant SCA effects, while their reciprocal crosses MV75 x MV142 and MV44 x MV142 displayed negative but not significant SCA. On the other hand, cross MV102 x MV75 exhibited negative significant SCA effects while its reciprocal exhibited positive and non-significant SCA effects.

4.3.4 Comparative assessment of F_1 hybrid seed, F_2 full-sib and F_2 half-sib generations of grain

4.3.4.1 Comparison based on hybrid/reciprocal cross response to weevil infestation

The list of the top 20 genotypes (hybrids/reciprocal crosses) that exhibited the highest level of resistance to weevil infestation, and the five most weevil susceptible genotypes is presented in Table 4.11. There were significant ($P < 0.05$) variations among hybrids/reciprocal crosses towards their response to weevil infestations, as manifested by F_1 weevil progeny emergence from F_1 hybrid seed, F_2 full-sib grain and F_2 half-sib grain. However, crosses MV75 x MV154, MV154 x MV142, MV142 x MV170, MV154 x MV31 and MV170 x MV13 were consistently ranked among the top 20 hybrids under the three seed/grain generations. On the other hand, cross MV102 x MV63 was consistently ranked among the bottom five hybrids under the three seed/grain generations. Most of the weevil resistant hybrids were generated from parental lines MV142, MV154 and MV170.

Table 4.11: List of top 20 and bottom five hybrids/reciprocal crosses, as regards to response to weevil infestation

F₁ hybrid seed		F₂ full-sib seed		F₂ half-sib	
Hybrid/check	F₁ weevils emerged	Hybrid/check	F₁ weevils emerged	Hybrid/check	F₁ weevils emerged
Top 20					
MV170 x MV13	6.00	MV142 x MV21	7.50	Check 2	8.17
MV75 x MV21	6.33	Check 2	10.50	Check 3	10.33
MV154 x MV142	6.70	MV170 x MV154	12.83	MV170 x MV44	12.50
MV154 x MV31	7.00	Check 3	13.13	MV170 x MV142	13.50
MV142 x MV170	7.00	MV170 x MV75	13.67	MV170 x MV31	14.00
MV75 x MV154	7.33	MV170 x MV21	20.33	MV31 x MV170	15.00
MV75 x MV102	7.33	MV21 x MV31	21.83	MV142 x MV13	15.83
MV13 x MV142	7.33	MV142 x MV170	23.67	MV170 x MV21	17.33
MV154 x MV102	7.60	MV170 x MV44	24.50	MV13 x MV75	18.00
MV142 x MV154	7.67	MV21 x MV170	25.33	MV170 x MV13	18.83
Check 3	7.70	MV63 x MV31	25.83	MV170 x MV63	19.33
MV63 x MV142	7.70	MV154 x MV170	26.50	MV142 x MV44	20.17
MV75 x MV31	8.00	MV13 x MV21	27.00	MV21 x MV154	21.16
MV63 x MV170	8.60	MV142 x MV154	27.83	MV154 x MV13	21.33
MV21 x MV102	8.70	MV75 x MV154	28.00	MV170 x MV102	21.83
Check 2	9.30	MV142 x MV13	28.83	MV63 x MV31	21.83
MV154 x MV13	9.60	MV63 x MV31	29.33	MV142 x MV170	22.67
MV63 x MV31	9.70	MV154 x MV31	29.67	MV142 x MV21	25.33
MV142 x MV13	9.70	MV63 x MV170	29.67	MV154 x MV142	25.67
MV154 x MV21	9.80	MV170 x MV13	30.33	MV75 x MV154	26.20
Bottom 5					
MV102 x MV44	32.00	MV102 x MV44	76.00	MV102 x MV63	64.00
MV44 x MV13	34.30	MV102 x MV63	77.33	MV102 x MV170	82.83
MV31 x MV170	45.00	MV44 x MV31	78.67	Check 7	102.00
Check 5	117.00	MV44 x MV75	79.18	MV102 x MV44	98.67
Check 7	122.00	Check 5	110.3	MV44 x MV21	
R²	0.89		0.72		0.84
CV (%)	50.20		39.30		31
LSD (0.05)	14.77		20.73		13.74
Mean	17.84		46.47		38.85

4.3.4.2 Comparison between generations based on sum of squares proportions

Results of the proportions of three genetic effects (GCA, SCA and REC) to the total genotype sum of squares for the three seed/grain generations are presented in Table 4.12. The results indicated that different genetic effects (combining ability effects) were manifested in each seed/grain generation. For example, in F₁ hybrid seed generation, reciprocal effects generally

constituted the largest proportion of the total genotype sum of squares which were 47.0, 36.7, 53.0 and 50.6% for FWE, MDP, DIS and PWM, respectively. On the other hand, the GCA effects constituted 22.0, 41.3, 20.0 and 24.3%, whereas SCA constituted 31.0, 22.0, 27.0 and 25.1% for FWE, MDP, DIS and PWM, respectively. For F₂ full-sib grain generation, generally GCA effects constituted the largest proportion of the total genotype sum of squares. The GCA percentages were 67.6, 57.9, 67.4, and 16.2% for FWE, MDP, DIS and PWM, respectively; while SCA and reciprocal effects were 21.6, 29.8, 24.2 and 38.5%, and 10.8, 14.0, 8.4 and 45.3% for FWE, MDP, DIS and PWM, respectively. For F₂ half-sib grain generation, on the other hand, the SCA effects constituted the largest proportion of the total genotype sum of squares. The proportions of SCA effects were 40.4, 55.0, 49.7, and 60.1% for FWE, MDP, DIS and PWM, respectively; while GCA and reciprocal effects were 27.4, 23.8, 28.5 and 9.7%, and 32.2, 21.2, 21.8 and 30.2 for FWE, MDP, DIS and PWM, respectively.

Table 4.12: Comparison of the proportions (%) of general combining ability, specific combining ability and reciprocal effects to the total genotype sum of squares for the three seed/grain generations

	F ₁ hybrid seed				F ₂ full-sib grain				F ₂ half-sib grain			
	FWE	MDP	DIS	PWM	FWE	MDP	DIS	PWM	FWE	MDP	DIS	PWM
GCAss	21.95	41.27	20.00	24.27	67.60	57.90	67.37	16.19	27.43	23.78	28.53	9.66
SCAss	31.02	21.99	27.00	25.11	21.60	29.81	24.23	38.51	40.39	55.03	60.12	60.12
RECss	47.03	36.74	53.00	50.61	10.80	14.03	8.40	45.30	32.18	21.19	30.22	30.22

FWE = F₁ weevils emerged, MDP = median development period, DIS = Dobie's index of susceptibility, PWM = parent weevil mortality, GCAss = general combining ability effects sum of squares, SCAss = specific combining ability effects sum of squares, and RECss = reciprocal effects sum of squares.

4.3.5 Narrow sense heritability (h^2) for F₁ weevil progeny emergence

The narrow sense heritability for F₁ weevil progeny emergence from F₁ hybrid seed, F₂ full-sib and F₂ half-sib grain are presented in Figures 4.1, 4.2, and 4.3, respectively. The narrow sense heritability for F₁ weevil progeny emergence was 7.9% in F₁ hybrid seed, 90.8% in F₂ full-sib seed, and 25.6% in F₂ half-sib grain.

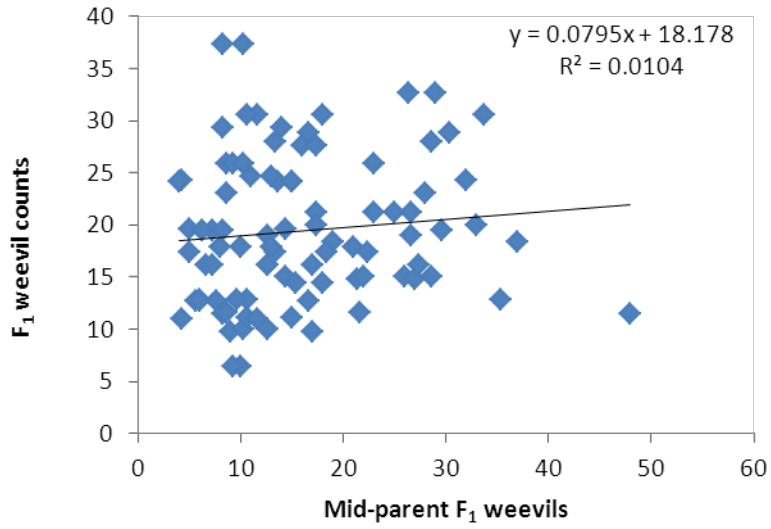


Figure 4.2: Narrow sense heritability for F₁ weevil progenies emerging from F₁ hybrid seed based on parent-offspring regression

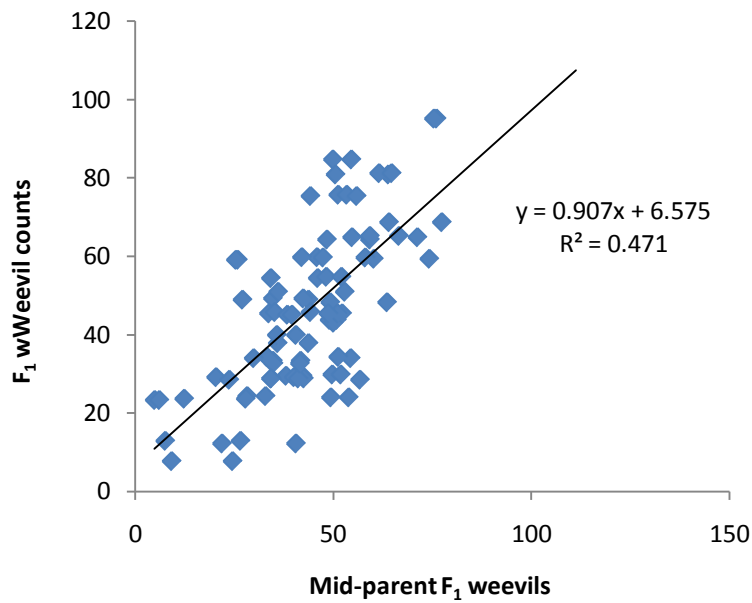


Figure 4.3: Narrow sense heritability for F₁ weevil progenies emerging from F₂ full-sib seed

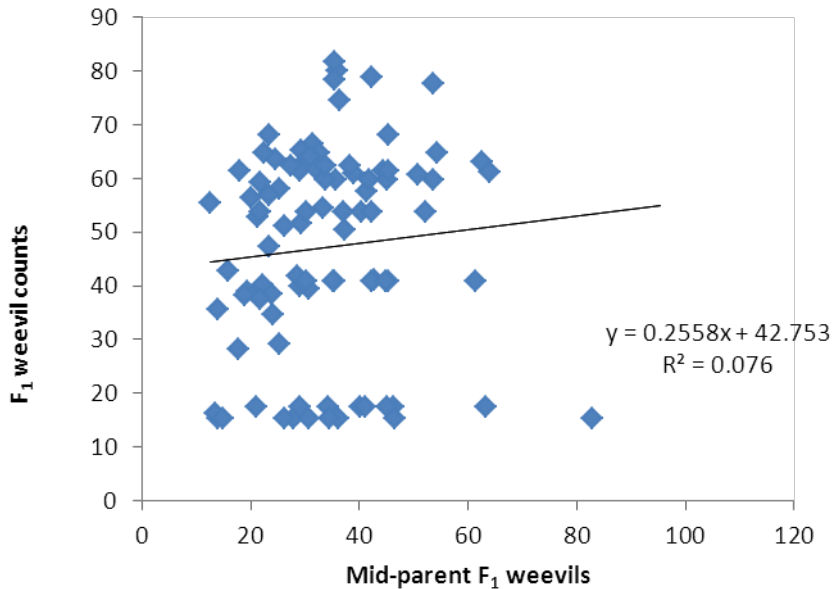


Figure 4.4: Narrow sense heritability for F₁ weevil progenies emerging from F₂ half-sib seed

4.4 Discussion

4.4.1 Combining ability effects and gene action exhibited towards F₁ weevil progeny emergence

The combining ability effects and gene action exhibited towards F₁ weevil progeny emergence median development period, Dobie's index of susceptibility and parental mortality in the ten parental lines and F₁ hybrid seed, F₂ full-sib grain, and F₂ half-sib grain are shown in Tables 4.3, 4.6, and 4.9, respectively. The significant genotype means squares for the study parameters indicated that the three categories of seed used for assessing weevil resistance all displayed significant differences in their response to weevil infestations, as regards to F₁ weevil progeny emergence, the median development period and parent weevil mortality. The significant GCA effects indicated that additive gene action was responsible for conditioning the weevil resistance parameters under the study (Tipping et al., 1989). The significant SCA effects on the other hand, revealed the governance of non-additive gene action in the expression of maize weevil resistance. For the significant reciprocal effects and its components, the maternal and non-maternal effects indicated significant differences in genotype response to weevil infestation resulting from the direction of the crosses made. This implies that if the resistant parent is used

as a female the resulting hybrid will be more resistant than when it is used as a male parent which is consistent with previous findings (Tipping et al., 1989). The significance of GCA, SCA, and reciprocal effects were in agreement with results reported by Kang et al. (1995) who observed additive, and non-additive gene action, and maternal effects in the governance of weevil non-preference in F_1 hybrids of a 10-parent diallel.

For F_1 weevil progeny emergence in F_1 hybrid seed, the reciprocal effects constituted 47.0% of genotype sum of squares, SCA effects contributed 31.0%, while GCA effects constituted 22.0%. This implied that maternal and non-maternal effects were involved and hence important in the governance of F_1 weevil progeny emergence in the F_1 hybrid seed. The influence of maternal effects is further enhanced through double fertilization (Faure et al., 2003). These results are consistent with Tipping et al. (1989) who reported significant maternal effects in F_1 hybrid seed, as opposed to seed in the subsequent generations. The results suggested that the maternal tissues, particularly, the endosperm were playing a big role in the resistance against the emerging F_1 weevil progenies.

Regarding the F_1 weevil progeny emergence in F_2 full-sib grain, the GCA effects were contributing 67.6% of the genotype sum of squares, SCA effects were contributing 21.6%, while reciprocal effects were contributing 10.8%. These results suggested the preponderance of additive gene action in the governance of F_1 weevil progeny emergence in F_2 full-sib grain. Regarding the relative importance of the genetic effects in F_2 half-sib grain, SCA effects were contributing the highest proportion (40.4%) of genotype sum of squares, as compared to GCA effects (27.4%) and reciprocal effects (32.2%). The high proportion of SCA effects could have arisen from the differences in flowering time manifested by specific hybrids. These results suggested the predominance of the non-additive gene action in conditioning hybrid resistance against weevil development and subsequent emergence of F_1 progenies from the F_2 half-sib grain.

The three seed categories exhibited differences for the type of gene action governing F_1 weevil progeny emergence, the median development period (MDP), Dobie's index of susceptibility (DIS), and parent weevil mortality. Overall, reciprocal effects were more important in the governance of the resistance parameters in F_1 hybrid seed, GCA effects were more important in the F_2 full-sib grain, while SCA effects were more important in F_2 half-sib grain. The cause of the variations in gene action in the three seed categories could be arising from seed size and differences in the maternal tissues and the sources of pollen used for fertilization. For instance,

the F_1 hybrid seeds are usually small seeded comprising of tissues (pericarp and endosperm) with two doses ($2n$) of the female inbred line parent and one dose (n) from the male (pollen source) inbred line. Therefore, the characteristics of F_1 hybrid seed are predominantly that of the female inbred line parent, thus the preponderance of the maternal effects based on the two gene doses.

On the other hand, the F_2 full-sib grain is relatively big seeded single cross hybrid seed whose endosperm comprises of two doses ($2n$) of constituents/genes from the single cross parent and one dose from the male parent of the same genetic composition (identity) as the female parent, implying that F_2 full-sib grain contains three doses ($3n$) of weevil resistance or susceptibility. Thus, through double fertilization genes responsible for weevil resistance are expected to accumulate in the F_2 full-sib grain by additive gene action. For the F_2 half-sib grain, it's only the female parent which is known, the pollen parent is random thus manifesting varying doses of resistance, depending on the characteristics of the pollen source. The dominance of SCA effects manifested in the governance of maize weevil resistance in F_2 half-sib grain showed the significance of non-additive gene action. The variations in response to weevil infestations exhibited by the different seed/grain generations demonstrated the need to sensitize farmers on appropriate seed management. Smallholder farmers usually have a tendency of recycling seed especially of landraces, open pollinated varieties, and to some extent hybrids. Therefore, the risk of decline in weevil resistance that may arise with advancements in seed generations needs to be put into consideration when recycling maize seed.

4.4.2 General combining ability effects exhibited in the study parameters

The ten parents exhibited differences in their general combining ability effects for responses to weevil infestations (Tables 4.3, 4.6, and 4.9). For F_1 weevil progeny emergence, genotypes exhibiting negative GCA effects were desirable. In this regard, parents MV170 and MV142 were significantly contributing to a reduction in the number of F_1 weevil progenies emerging from the F_1 hybrid seed. This suggested that parents MV170 and MV142 would be suitable parents for enhancing weevil resistance when breeding for weevil resistance.

For the median development period, genotypes that took longer periods for the weevils to develop and emerge were desirable because weevils would also take longer to multiply. Thus cause less damage to the grain in the same time period than if they had multiplied quickly. Therefore, positive GCA effects were desirable as they would lead to an increment in weevil

development periods. Consequently, seed from F_1 hybrid parents MV21, MV154, MV31, MV170 and MV142 which exhibited positive significant GCA effects were desirable because once they were infested the weevils would take longer to develop and multiply. The same parents MV21, MV154, MV31, MV170 and MV142 exhibited positive and significant GCA effects in F_2 half-sib seed, while parents MV154, MV31, MV170 and MV142 exhibited positive significant GCA effects and thus were desirable from F_2 full-sib grain.

For parental weevil mortality, positive GCA effects lead to an increase in weevil death, therefore parents MV63, MV170 and MV142 with positive and significant GCA effects exhibited an increase in parent weevil mortality in F_1 hybrid seed, parent MV21 was desirable under the F_2 full-sib grain category, while parent MV63 was desired under F_2 half-sib grain category. For parent weevil mortality parameters, parents that exhibited negative and significant GCA effects were not desirable as they would lead to a reduction in parent weevil mortality. Therefore, parents MV31 and MV44 in the F_1 hybrid seed; parents MV31, MV44, and MV102 in the F_2 full-sib seed; and parent MV21 from F_2 half-sib seed were associated with a decline in parent weevil mortality. This implies that more parental weevils would survive and multiply in the hybrids derived from the two parents.

Based on the general combining ability results, discrimination of parents into the ones associated with weevil resistance and the ones associated with weevil susceptibility, three resistance parameters F_1 weevil progeny emergence, median development period, and Dobie's susceptibility index consistently categorized the study parents into resistance and susceptible groups for the F_1 hybrid, F_2 full-sib and F_2 half-sib generations.

4.4.3 Specific combining ability effects

Results of the specific combining ability effects as revealed by F_1 weevil progeny emergence, the median development periods, Dobie's index of susceptibility, and parental weevil mortality exhibited in F_1 hybrid seed, F_2 full-sib and F_2 half-sib grain, showed varying responses.

Generally, for F_1 weevil progeny emergence, manifestation of negative and significant SCA effects implies a significant reduction in the F_1 weevil progenies emerging out of a particular cross. Therefore, negative and significant SCA effects are desirable for weevil resistance breeding.

For the median development period (MDP), hybrids that exhibit longer periods for the F_1 weevil progenies to develop and emerge are desirable, over hybrids that allow faster development and emergence of F_1 weevil progenies. Therefore, hybrids that manifested positive and significant SCA effects were desirable because they were contributing towards extending MDP.

As regards to parental weevil mortality, the more the parental weevils die the fewer the F_1 weevils and the lesser the grain damage will be encountered. Therefore, hybrids that exhibit high values of parental weevil mortality are desirable over the ones enhancing the survival of parental weevils. Thus hybrids that exhibited positive and significant SCA effects for parental weevil mortality are desirable against hybrids that exhibited negative SCA effects.

On the other hand, for Dobie's index of susceptibility, the lower the indices the more the resistance exhibited by the hybrid. Negative and significant SCA effects indicated significant reductions in DIS values. Accordingly, hybrids that displayed negative and significant SCA effects for DIS were desirable over those with positive indices.

Various crosses displayed negative significant SCA effects towards F_1 weevil progeny emergence in the three seed categories. However, some of the crosses exhibited differences in the manifestation of the SCA effects, resulting from the direction of the cross. For example, cross MV142 x MV102 in the F_1 hybrid seed category exhibited negative significant SCA effects; while its reciprocal cross (MV102 x MV142) exhibited positive significant SCA effects. The same occurrence was manifested in F_2 half-sib grain, but was not observed in F_2 full-sib seed. These results suggest the presence of maternal effects in the expression of alleles responsible for weevil resistance. The results are in agreement with Tipping et al. (1989), who reported significant maternal effects in F_1 hybrid seed, but not in F_2 hybrid (full-sib) grain. This implies that during seed production, when selecting parents for different crosses, the seed parents need to be weevil resistant, in order to be able to resist weevil infestations especially during storage.

The occurrence of maternal effects in F_1 hybrid seed and F_2 half-sib grain is likely to have resulted from double fertilization exhibited during embryo and endosperm development (Faure et al., 2003). Double fertilization leads to an endosperm with two doses of the genetic materials from the seed parent (female) and one dose of genetic materials from the pollen parent. For the F_1 hybrid seed and F_2 half-sib seed, maternal effects were manifested mainly between crosses of resistant parents MV142 and MV170 and susceptible parents MV44 and MV102 (Table 4.3). When the resistant parent, for example MV142 was used as a seed parent, and the susceptible

parent MV102 used as a pollen parent, the resulting hybrid (MV142 x MV102) possessed two doses of weevil resistance alleles from MV142. On the other hand, when the seed parent was MV102, and crossed with MV142, the hybrid (MV102 x MV142) possessed only one dose of resistance alleles from the male parent. This phenomenon could have resulted into the significance of maternal effects.

Another type of response exhibited was the manifestation of weevil resistance in a hybrid generated from a cross between a susceptible female parent (2n) and a resistant male parent (n), this phenomenon would imply that two doses of susceptibility genes were combined with one dose of resistance genes to generate a resistant hybrid. For example crosses MV44 x MV142, MV44 x MV21, MV44 x MV75, MV44 x MV170, MV102 x MV142, and MV102 x MV21 these results revealed the influence of non-additive (dominance) gene action.

4.4.4 Comparative assessment of F₁ hybrid seed, F₂ full-sib and F₂ half-sib generations of grain

High levels of consistency were exhibited when ranking the top 20 hybrids/reciprocal crosses that were resistant to weevils (Table 4.11). Consequently, hybrids/reciprocal crosses MV75 x MV154, MV154 x MV142, MV142 x MV170, MV154 x MV31, and MV170 x MV13 were ranked among the top 20 hybrids under the three seed/grain generations by F₁ weevil progeny emergence as the evaluation parameter. Similarly, hybrid MV102 x MV44 was consistently ranked among the worst five hybrids/reciprocal crosses. Based on F₁ weevil progeny emergence, any grain generation could be used for purposes of discriminating maize genotypes into different response classes.

Hybrids MV170 x MV13 and MV75 x MV154 were ranked among the top 20 weevil resistant (Table 4.11) as well as among the top 20 stable high yielding hybrids/reciprocals (Chapter Five, Table 5.4). Therefore, the two genotypes are good candidates for further evaluations regarding the two traits.

As regards to the significance of the genetic effects/combining ability effects towards weevil resistance, variations were observed among seed/grain categories (generations) for the proportions of GCA, SCA and reciprocal effects to the total genotype sum of squares (Table 4.12). For F₁ hybrid seed the reciprocal effects were the most important genetic effects, this was probably because of the maternal effects manifested in the pericarp and endosperm of the F₁

hybrid seed, which is basically parental line seed comprising of two doses of the genetic materials from the seed parent and only one dose from the pollen parent. These results are in agreement with findings by Tipping et al. (1989), who reported significant maternal effects in F_1 hybrid seed generated from a 10 x 10 full diallel cross scheme. For F_2 full-sib grain, GCA effects were generally the most important genetic effects, thus indicating the predominance of additive gene action. This was probably because F_2 full-sib grain comprises of three doses of the same genetic materials from both seed and pollen parents, which are F_1 hybrid tissues in the pericarp, endosperm and embryo. On the other hand, SCA effects were the most important effects in F_2 half-sib grain; probably because of the random pollen from different pollen parents, which may give rise to a range of genetic combinations of varying doses of genetic materials. It is anticipated that a smaller proportion of plants would flower earlier and/or later than the rest, and hence higher chances of undergoing through self pollination, while the plants that flower in the middle of the flowering period would be more and hence higher chances of out-crossing with almost every plant. Thus, the preponderance of SCA effects is likely to be resulting from the flowering time (out-crossing). The significant GCA and SCA effects are consistent with Kang et al. (1995) findings.

4.4.5 Narrow sense heritability (h^2)

The low narrow sense heritability (7.9%) for the F_1 weevil progeny emergence manifested in F_1 hybrid seed indicated low influence of additive gene action (indeed maternal effects were predominant in F_1 hybrid seed), suggesting that selection would not be effective towards maize improvement for weevil resistance when based on the F_1 generation. As regards the F_2 half-sib generation, the low narrow sense heritability (25.6%) that was due to the random pollen, contributed to the high dominance variance (V_D), which would render selection less effective in improving F_2 half-sib against weevil infestation. On the other hand, the high narrow sense heritability (90.8%) exhibited in F_2 full-sib generation indicated the influence of additive gene action because only the additive variance (V_A) is fixed when F_1 was mated with F_1 in the same cross while V_D was not fixed; and thus selection would be effective in the improvement of F_2 full-sib generation for weevil resistance.

4.5 Conclusion

The results revealed that additive gene action, non-additive gene action and maternal effects were all responsible for conditioning weevil resistance in F_1 hybrid seed, F_2 full-sib and F_2 half-sib grains derived from the 10 x 10 full diallel mating scheme. Parents MV170 and MV142 were significantly contributing towards a reduction in weevil emergence in F_1 hybrid seed, F_2 full-sib and F_2 half-sib grain hence they were good general combiners. This was further portrayed by the high levels of heterosis exhibited in hybrids generated by the two parents. Considering the top 20 weevil resistant hybrids/reciprocal crosses, a large proportion of hybrids listed were generated by the two parents.

Hybrids MV75 x MV154, MV154 x MV142, MV142 x MV170, MV154 x MV31 and MV170 x MV13 were consistently ranked among the top 20 weevil resistant hybrids based on the F_1 weevil emergence from the three seed/grain generations, therefore they are recommended for advanced evaluations for yield, weevil resistance and other farmer-desired traits.

Crosses MV75 x MV142, MV142 x MV44, MV75 x MV142, and MV31 x MV102 exhibited significant and negative SCA effects in more than one generation of seed/grain and therefore they would be appropriate cross combinations for evaluations across generations.

Generation of resistant hybrids from crosses between resistant and susceptible parents suggested the influence of non-additive gene action arising from the $2n \times n$ gamete fusion. Conversely, generation of maize weevil resistant hybrids from crosses between susceptible and resistant parents suggested the influence of additive gene action, possibly resulting from the presence of resistance genes being masked within susceptible parents.

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Appendices

Appendix 4.1: Specific combining ability estimates exhibited in the F₁ hybrid seed using the median development period

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		-3.92*	-1.30	3.13	0.22	1.08	3.15	0.43	0.55	0.28
MV154	-0.83		1.77	-0.47	0.28	-1.18	1.22	5.67***	-0.22	0.88
MV31	-4.83**	-2.50		-0.35	-1.27	0.77	1.67	0.95	-1.93	-0.07
MV44	1.50	2.17	5.33**		-1.33	-2.47	0.43	0.55	0.67	5.67
MV13	3.83*	3.83*	-2.00	-0.83		-0.05	-2.48	1.80	1.58	6.75*
MV63	2.67	2.00	1.00	0.67	3.67*		1.05	-1.00	1.78	1.38
MV75	5.00**	-0.33	6.17***	-1.17	1.50	-2.00		2.90	0.52	-2.02
MV102	5.33**	0.83	2.17	0.33	2.17	-1.67	2.17		-2.37	0.37
MV170	-3.00	-0.50	-4.17*	-4.67*	-3.50	-3.00	-4.00*	-1.83		-1.75
MV142	-3.17	2.83	0.83	-5.00**	-3.83*	0.17	1.50	-3.17	5.17**	

Appendix 4.2: Specific combining ability exhibited in F₁ hybrid seed as portrayed by Dobie index of susceptibility

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		2.77**	2.42*	-2.23*	-0.66	-1.26	-2.17*	-1.73	0.12	2.73**
MV154			-0.02	-0.06	-0.75	1.31	0.90	-2.15*	-1.20	-0.80
MV31				-2.39*	1.79	0.59	-2.64**	-0.58	2.31*	-1.47
MV44					2.46*	0.46	0.68	0.14	0.60	0.33
MV13						-1.62	0.92	-1.06	0.04	-1.12
MV63							1.30	1.58	-0.87	-1.50
MV75								-0.95	0.61	1.34
MV102									1.32	3.43***
MV170										-2.94**
MV142										

Appendix 4.3: Specific combining ability for parental weevil mortality in F₁ hybrid seed

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		-0.86	1.89	1.09	4.23*	1.19	2.58	-4.91**	0.58	6.05
MV154	-6.17**		0.46	-2.51	4.29*	4.09*	2.64	-3.01	4.98**	0.82
MV31	-8.67***	3.00		-3.42	-3.79*	-0.49	5.89**	5.91**	-4.27*	7.07*
MV44	0.33	0.500	1.00		1.74	7.38***	0.43	-2.06	-3.91*	1.70
MV13	8.33***	2.83	2.16	-6.17**		-1.49	-6.94***	1.91	-3.11	2.40
MV63	-1.50	-11.50***	-9.33***	-10.67***	-4.00		-2.81	-2.79	0.03	4.93
MV75	-6.83**	-10.67***	-4.33*	0.00	-0.17	2.83		6.93***	1.58	9.55**
MV102	0.67	-5.67**	2.00	1.50	-2.00	6.17**	0.17		3.09	10.70**
MV170	-7.00***	-3.17	-6.33**	-3.17	-7.50***	-6.17**	-1.33	-7.17***		-4.45
MV142	-4.17*	1.17	6.00**	-7.50***	3.33	0.00	-0.33	-9.50***	0.833	

Appendix 4.4: Specific combining ability for median development period in F₁ hybrid seed

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		-0.78	0.49	0.14	-0.47	-2.20**	0.42	1.57*	-0.60	1.01
MV154	-0.67		-0.25	-0.02	-0.21	0.73	0.18	0.24	1.66*	0.67
MV31	1.67	-0.08		1.59*	0.90	1.09	-0.13	-0.73	-0.07	-0.44
MV44	-0.33	1.00	-0.17		0.29	1.39	-0.17	-2.67***	3.41***	6.92***
MV13	-1.58	0.67	0.50	-0.92		-0.46	0.49	2.23**	-0.11	-0.07
MV63	0.67	-0.42	1.33	-1.67	-2.17*		0.43	-0.17	-0.01	0.75
MV75	0.50	0.25	0.33	-0.67	0.17	-0.25		1.36	-0.64	2.13
MV102	0.00	0.50	0.75	0.67	0.25	1.00	-0.42		-1.07	-0.60
MV170	-1.8*	-1.67	-0.33	-0.17	0.83	-1.08	-0.17	-0.25		2.57
MV142	-1.00	0.67	0.00	1.83*	0.50	1.00	0.00	-0.75	1.17	

Appendix 4.5: Specific combining ability for Dobie index of susceptibility exhibited in F₂ full-sib seed

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		0.31	0.41	0.06	0.30	0.80	-0.18	-0.28	1.10**	-0.56
MV154	-0.54		0.07	-0.02	0.02	-0.37	-0.32	-0.33	-0.18	-0.17
MV31	-1.26**	0.50		-0.48	-0.36	-0.56	0.45	0.53	-2.43***	0.83
MV44	-0.15	-0.23	0.16		-0.34	-0.76	-0.09	0.52	-0.99*	-2.69***
MV13	0.93*	0.23	-0.18	0.38		-0.52	-0.68	-0.75	1.15**	0.14
MV63	-0.03	-0.23	-0.75	0.31	0.57		-0.15	0.16	0.74	-0.26
MV75	-0.61	-0.27	-0.03	0.13	-0.27	-0.01		-0.57	0.36	0.54
MV102	-0.29	0.13	-0.55	-0.21	0.24	-0.43	-0.07		0.83*	0.50
MV170	0.74	0.82	-0.24	0.06	-0.36	-0.13	0.74	0.27		0.55
MV142	1.26**	-0.13	0.00	-0.29	0.18	-0.32	0.04	0.36	-0.57	

Appendix 4.6: Specific combining ability for parent weevil mortality exhibited in F₂ full-sib seed

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		0.31	-0.83	-1.92	-0.78	0.65	-0.56	-0.55	4.35***	3.31
MV154	0.33		0.65	-4.18***	-0.30	3.47**	-0.24	-0.40	0.59	-3.51
MV31	2.25	-0.08		-1.33	-1.78	-0.85	-0.31	0.95	-0.56	-2.27
MV44	1.67	-0.25	0.33		3.30**	0.40	2.61*	1.78	0.43	-2.78
MV13	1.33	-1.33	-0.92	-3.83**		-1.38	-2.34	1.67	0.90	-1.16
MV63	4.33**	-1.33	-0.08	-2.00	-2.42		-1.24	-2.31	-1.00	-1.01
MV75	-1.33	-2.17	-0.67	-0.25	0.67	-0.17		-2.70*	-1.54	-8.13***
MV102	2.08	1.92	1.67	2.00	-0.42	0.33	1.67		-0.70	-1.56
MV170	1.75	1.17	-4.58***	-3.58**	-2.92*	-3.08*	3.42*	-4.50**		-0.87
MV142	-0.33	1.33	-1.83	-2.83*	-0.92	-2.00	-0.17	-2.17	2.58	

Appendix 4.7: Specific combining ability for median development period exhibited in F₂ half-sib seed

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		2.16***	1.42*	1.44*	1.25*	1.14	0.40	0.39	0.59	14.87***
MV154	2.33***		1.07	1.59*	0.74	1.45*	0.39	1.54**	0.08	10.38***
MV31	1.5*	1.67*		0.51	1.08	1.63**	0.48	1.54**	1.75**	10.88***
MV44	1.92**	0.75	1.25		1.76**	-0.19	1.91**	0.31	0.02	8.94***
MV13	1.58*	0.58	0.17	1.08		1.38*	0.23	1.13	-0.08	11.21***
MV63	0.58	0.25	2.00**	0.58	1.17		1.28*	-0.41	2.47***	9.74***
MV75	3.00***	2.83***	1.50*	3.00***	2.50***	1.17		0.69	1.74**	6.98***
MV102	4.33***	3.17***	4.08***	1.92**	3.08***	1.67*	1.58*		-7.07***	7.83***
MV170	2.25***	-1.58*	-0.33	0.33	-2.42***	-2.08**	-2.50***	-4.08***		9.62***
MV142	1.83**	0.50	-0.92	-0.08	-1.00	-0.58	-1.33*	-3.33***	-1.42*	

Appendix 4.8: Specific combining ability for Dobie index of susceptibility in F₂ half-sib seed

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		-0.79**	-0.10	-0.33	-0.16	-0.48	-0.23	-0.21	-0.01	-3.58***
MV154	-0.79**		-0.58*	-0.50	-0.54*	-1.07***	0.15	-1.00***	0.30	-3.08***
MV31	-0.86**	0.29		-0.24	0.06	-1.03***	-0.15	-0.83**	-0.71**	-3.97***
MV44	-1.33***	-0.75*	-0.24		-0.52*	-0.22	-0.69**	-0.25	-0.68*	-3.37***
MV13	-0.33	-0.05	-0.25	0.10		-0.93***	-1.51***	-0.81**	0.69**	-4.33***
MV63	-0.18	0.28	-0.13	-0.30	-0.23		-0.28	0.56*	-0.32	-3.91***
MV75	-1.20***	-1.37***	0.20	-0.33	-0.69*	0.25		-0.56*	-0.60*	-2.83***
MV102	-1.10***	-0.56	-1.56***	-0.54	-0.36	-0.46	-0.88**		0.56*	-3.31***
MV170	0.09	0.76**	-0.23	1.07***	0.77**	0.87**	0.76**	2.11***		-1.95***
MV142	-0.28	-0.25	1.22***	1.25***	1.24***	-0.00	0.79**	1.26***	0.15	

Appendix 4.9: Specific combining ability for parent weevil mortality in F₂ half-sib seed

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		-0.00	-0.11	-0.20	0.16	0.01	0.15	0.12	-0.13	0.07
MV154	0.10		0.11	0.23	-0.10	-0.22	0.16	0.03	-0.28	0.02
MV31	-0.24	-0.06		0.17	-0.22	-0.13	-0.06	0.26	0.25	-0.08
MV44	-0.20	-0.01	0.04		-0.13	0.20	-0.02	0.39*	-0.11	0.72*
MV13	0.01	-0.06	-0.13	0.22		-0.10	0.22	-0.18	-0.00	0.11
MV63	0.14	-0.09	0.02	0.18	-0.15		-0.30	0.36*	-0.06	-0.10
MV75	0.01	0.19	0.12	0.22	-0.01	0.07		-0.51**	0.05	-0.65*
MV102	-0.02	0.13	-0.01	0.40*	0.18	0.11	0.11		0.12	0.38
MV170	-0.18	-0.05	0.11	-0.14	-0.29	-0.08	0.04	0.21		-0.30
MV142	0.19	-0.01	-0.27	-0.26	0.25	-0.09	-0.01	0.03	0.27	

Chapter Five

Diallel analysis for yield and secondary traits in eastern and southern Africa maize germplasm lines

Abstract

Maize productivity in Uganda like other countries sub-Saharan African countries is still very low at farmer level as opposed at research level. This study endeavored to contribute to this cause through identification and utilization of adaptable elite maize germplasm with high yield potential. The study objectives were to: i) determine the combining ability and gene action governing grain yield in maize weevil resistant lines from eastern and southern Africa maize germplasm, and ii) identify inbred lines with good combining ability for grain yield. Ten parental inbred lines with good agronomic characteristics, resistance to maize weevil and foliar diseases were crossed in a 10 x 10 full diallel mating design. The 45 experimental hybrids and their reciprocals generated were evaluated together with their ten parental lines under four environments. The general combining ability (GCA), specific combining ability (SCA), and reciprocal effects were all significant for grain yield, with SCA accounting for over 80.0% of hybrid sum of squares. For secondary traits, GCA was only significant for ear aspect but not significant for grain texture, plant and ear height; whereas, SCA was significant for all secondary traits in the study. However, reciprocal effects were not significant for secondary traits. Heterosis ranged from 81.3% to 365.2% using the better parent method, suggesting that the study germplasm exhibited adequate genetic diversity that would be useful for hybridization. Inbred line parent MV44 exhibited positive significant GCA for grain yield and thus can be utilized in the development of synthetics and hybrids; while crosses between parents MV21 x MV13, MV154 x MV44, and MV154 x MV102 displayed significant SCA, hence suggesting that the parents involved are suitable for hybrid development. Parent MV142 exhibited significant positive SCA effects with the rest of the other nine parental lines, but did not display significant GCA effects. Overall the results demonstrated the parental lines' potential towards grain yield enhancement through hybridization.

Key words: Combining ability, heterosis, inbred lines, and maize productivity.

5.1 Introduction

Maize (*Zea mays* L.) is an important food and cash crop worldwide; it is the third most important crop next to wheat and rice. Maize is one of the most important staple food crops in sub-Saharan Africa and grown by both small and large scale farmers. In Uganda, maize is the most important cereal crop with increasing importance as food and cash crop, being a major crop commodity on the market in the eastern Africa region (Benson et al., 2008). In spite of its increasing importance, maize productivity in Uganda is still low with an average yield of only 1.5 t ha⁻¹ compared to 4.7 t ha⁻¹ in South Africa (FAOSTAT, 2010). Like in a number of other countries, the increase in maize production is mainly a result of an increased area under maize cultivation, but not necessarily an increase in its productivity or yield *per se*, and this is rather unsustainable considering the high population growth rate and limited amount of land leading to increased space and food requirements.

The low maize productivity is attributed to a number of factors including: drought and nitrogen stress (Bänziger and Diallo, 2001; Makumbi et al., 2011), Stem borers (Kalule et al., 2006; Kalule et al., 1997) and diseases like *Turcicum* leaf blight (Adipala et al., 1993), grey leaf spot (Bigirwa et al., 2000) and rust among other major diseases causing considerable yield losses in maize. Development of adaptable high yielding disease resistant maize cultivars would provide a sustainable remedy to the low maize productivity. Utilization of maize germplasm from different genetic background enhances heterosis and thus increases the chances of generating outstanding stress tolerant hybrids (Makumbi et al., 2011). However, prior knowledge of the characteristics of putative germplasm is paramount (Bernardo, 2003). Consequently, availability of information on the genetic variability in yield and secondary traits, pest and disease resistance, and the gene action conditioning the expression of desired traits under different environmental conditions would be vital for the development of elite maize cultivars.

Several studies have been conducted on the genetics and expression of different traits in maize including grain yield (Onwubiko and Onwubiko, 2011). Ultimately, information has been generated on a numbers of aspects of which combining ability and/or gene action for different traits under various environments involving both stress and stress-free conditions (Lee et al., 2003; Makumbi et al., 2011; Fato et al., 2012). Makumbi et al. (2011) conducted combining ability studies for drought and nitrogen stresses under stress and non-stress conditions for 15 tropical inbred lines together with their experimental hybrids derived from a diallel mating design and reported stress dependent gene action for yield. They observed significant general

combining ability (GCA) effects under adequate moisture and water-stressed environments; whereas specific combining ability (SCA) effects were important under low nitrogen-stress conditions. Another study was conducted under downy mildew conditions, and both GCA and SCA were reported to be governing grain yield (Fato et al., 2012). Similar results were reported by Lee et al. (2005) from studies on dry matter accumulation during grain filling and ultimately grain yield. However, the information generated on the genetics of a number of traits usually applies to a specific type of germplasm and environment (Falconer, 1981); thus the need to generate information on the genetics of maize weevil resistance in the study maize germplasm, under environmental conditions that are representative of the target environment where the final cultivars would be deployed.

This study was undertaken to evaluate the potential of maize germplasm lines from eastern and southern Africa which had been selected for weevil resistance, in developing adaptable hybrids with outstanding yield in Uganda. This study was designed to generate information on combining ability and gene action conditioning the expression of yield and secondary traits, in addition to studies on their heritability and heterosis. The objectives of the study were to: i) determine the combining ability and gene action conditioning grain yield in maize germplasm from the eastern and southern Africa region and identify adaptable hybrids. ii) identify elite adaptable weevil resistant inbred lines with good combining ability for grain yield enhancement. The inbred lines had first been screened for weevil resistance (see Chapter Four, Section 4.2.1), then crossed and the resulting hybrids were evaluated for both yield and weevil resistance.

5.2 Materials and Methods

The study materials constituted of parental lines at advanced stages of evaluation, obtained from eastern and southern Africa maize germplasm. They were selected from the foregoing maize screening trial that was conducted in 2010B season at the National Crops Resources Research Institute (NaCRRI), Namulonge, Uganda. They comprised germplasm obtained from the National Maize Breeding Program, NaCRRI and from the International Maize and Wheat Improvement Center (CIMMYT-Kenya) which constituted germplasm from eastern Africa; while parental lines from southern Africa region were acquired from the University of KwaZulu Natal, Republic of South Africa.

A selection index was used to select the best two inbred lines from South Africa and the best three inbred lines from Uganda and CIMMYT-Kenya (three from each source). The major traits considered in the index were: weevil resistance, low foliar diseases scores, agronomic superiority, and yield. Additionally, two weevil susceptible inbred lines with good agronomic performance were added to get a total of ten inbred line parents (Table 5.1). The ten parental lines were crossed in a 10 x 10 full diallel mating design. The nurseries were planted in March, 2011A season at NaCRRI, Namulonge (1200 m.a.s.l); 0°32'N, 32°34'E; 1300 mm bimodal rainfall. To provide for cultivar differences in flowering period, three staggered plantings were made at intervals of five days between each planting, this ensured adequate synchronization of silking and pollen shed among the parental lines.

Table 5.1: Genotype names, pedigrees, origin and characteristics of parents used in the 10 x 10 full diallel mating design

Genotype number	Pedigree/parents	Origin	Response to weevils
MV21	CML507	CIMMYT	Resistant
MV154	WL429-27	Uganda	Resistant
MV31	[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-B//EV7992/EV8449...-3-2-2-1-BBBBB-B-B-B	CIMMYT	Resistant
MV44	[(CML395/CML444)-B-4-1-3-1-B/CML444//[[TUXPSEQ]C1F2/MV449-SR]F2-45-7-1-2-BBB]-2-1-2-2-BBB-B-B-B	CIMMYT	Susceptible
MV13	CKL05019	CIMMYT	Resistant
MV63	09MAK17-15-1	South Africa	Resistant
MV75	09MAK17-28-1	South Africa	Resistant
MV102	09MAK9-157	South Africa	Susceptible
MV170	WL118-9	Uganda	Resistant
MV142	WL-118-3	Uganda	Resistant

5.2.1 Field evaluations

The genotypes evaluated in 2011B and 2012A seasons were: the 45 experimental hybrids generated from the 10 x 10 full-diallel mating scheme and their reciprocals (45), the ten parental lines used in the crossing scheme, and six standard checks. The standard checks used were: Longe5, one of the most popular open pollinated varieties in Uganda (check 1); two weevil

resistant genotypes from CIMMYT-Zimbabwe, [Genotype#10 [weevil/CML312]-B-13-2-1-BBB/[weevil/CML387]-B-9-1-1 and Genotype # 11 07WEEVIL (CIMMYT HA1091)], coded as CIMMYT-Zim10 and CIMMYT-Zim11 as checks 2 and 3, respectively; Longe10H, a popular three-way cross hybrid in Uganda (check 4); MM3, an extra early maturing open pollinated variety (check 5); and Longe6H, another popular three-way cross hybrid in Uganda (check 6). Additionally, single cross tester hybrids A (CML312/CML442) and B (CML202/CML395) were added to make a total of 108 genotypes. The 108 genotypes were evaluated in four environments. The sites were National Crops Resources Research Institute, Namulonge (0°32'N, 32°34'E, 1200 m.a.s.l) for two environments in 2011B and 2012A seasons; Masaka District Agricultural Technology Development Centre, Kamenyamiggo (0°18'18.2" S, 31°39'50.1" E, 1253 m.a.s.l) planted in season 2011B; and the National Semi-Arid Resources Research Institute, Serere (1° 32'N, 33°27'E, 1140 m.a.s.l) also planted in season 2011B.

The field trial was arranged in a 12 x 9 alpha lattice design with two replications laid side by side. Single row plots were used. The plot sizes were 5 m long, the inter-row spacing was 0.75 m while the intra-row spacing was 0.30 m, thus giving a plant population of 44,444 plants ha⁻¹. Fertilizers were applied at the rate of 33 kg P and 120 kg N ha⁻¹, provided in the form of Di-ammonium phosphate and urea, respectively.

The secondary traits measured included; plant and ear heights, the number of ears per plant, ear aspect and grain texture. Plant height (cm) was determined by measuring the distance from the base of the maize plant to the first tassel branch. It was determined when all plants had flowered that is after attaining maximum height. Ear height (cm) on the other hand, was determined as the distance from the plant base to the node where the upper ear is attached to the plant. For ear aspect, the assessment was done after harvesting. Ears for each genotype were arranged in the same orientation in such a way that all ears could be seen and scored at once; a scale of 1 to 5 was used, where 1 = very good, assigned to big uniform and appealing cobs with flint kernels; 2 = good, assigned to big fairly uniform cobs with less flint kernels; 3 = average, assigned to fairly uniform cobs of average size with semi-flint/semi-dent kernels; 4 = poor, small non-uniform cobs with more of dent kernels; 5 = very poor, assigned to cobs with inferior characteristics such as small non-uniform cobs with gaps and/or uneven kernels.

After scoring for ear aspect, the genotypes were then scored for grain texture using a scale of 1 - 5 where: 1 = 100.0% shiny-flint kernels, 2 = semi-flint (flint kernels with less than 25.0% dent kernels), 3 = semi-flint-semi-dent (26.0 to 50.0% dent kernels), 4 = semi-dent (51.0 - 75.0% dent

kernels), and 5 = dent (76.0 to 100.0% dent kernels). Finally representative grains were sampled from each ear for the estimation of grain moisture content (MC). All ears were weighed to establish the field weight for each genotype. Yield (t ha^{-1}) for each genotype was calculated using the formula in Section 3.2.4.

5.2.2 Data analysis

The performance of the 45 experimental hybrids and their reciprocals was compared to that of the local checks across the 4 environments using SAS version 9.1 procedure general linear models (SAS-Institute, 2003). Cultivar stability across the 4 environments was estimated based on grain yield (the ultimate trait of interest). Additive main effects and multiplicative interactions (AMMI) under Genstat version 14 was used for analyzing genotype by environment interaction (GxE) and subsequently genotype stability was assessed based on GxE results. Stable high-yielding cultivars were identified using the “Genotype Selection Index (GSI)” that integrates both cultivar stability and yield in its formula (Farshadfar, 2008). The genotype selection index was generated as: $\text{GSI} = \text{RASV} + \text{RY}$, where RASV = rank of AMMI stability value, RY = rank of mean grain yield of genotypes. RASV was obtained after calculating AMMI stability values (ASV) using the formula $\text{ASV} = \sqrt{[\text{SS}_{\text{IPCA1}}/\text{SS}_{\text{IPCA2}}(\text{IPCA1 score})]^2 + (\text{IPCA2 score})^2}$.

Where, $\text{SS}_{\text{IPCA1}}/\text{SS}_{\text{IPCA2}}$ is the ratio of the sum of squares for IPCA1 and IPCA2, which are obtained from AMMI analysis. Rank of mean for grain yield of genotypes (RY) was performed using the mean grain yield values for each cultivar, obtained across the 4 environments. The GSI values calculated for each genotype were ranked from the smallest to the largest. The smaller the GSI value was, the more stable and high yielding the cultivar was across environment.

For data on the genetics of grain yield, grain texture, ear aspect, plant and ear heights were subjected to Griffing’s method 1 model 1, for estimating the general and specific combining abilities, reciprocal effects, maternal and non-maternal effects of the 10 parental lines crossed in a full-diallel mating scheme (Griffing, 1956). Data on the above mentioned traits, from the 45 experimental hybrids, and their 45 reciprocal crosses, and the 10 parental lines (total 100 genotypes) were subjected to diallel SAS05 program; the genotypes were considered as fixed effects, while the environments and replications within environments were considered as

random effects and therefore tested against the residual error term (Zhang et al., 2005). The model used in the analysis was:

$$Y_{ijkl} = \mu + g_i + g_j + r_{ij} + s_{ij} + \frac{1}{bc} \sum_k \sum_l e_{ijkl},$$

where Y_{ijkl} = observed measurement for the ij^{th} cross in the k^{th} replication, under l^{th} environment, μ = is the population mean; g_i and g_j = General combining ability (GCA) effects for the i^{th} and j^{th} parental lines, respectively; r = reciprocal effects, such that $r_{ij} = -r_{ji}$; s_{ij} = Specific combining ability (SCA) effect for the ij^{th} cross; and e_{ijkl} = error term associated with the ij^{th} cross evaluated in the k^{th} replication, under l^{th} environment.

The sums of squares for the estimates of the GCA, SCA and reciprocal cross effects were computed and their relative significance in contributing to the overall phenotypic variation determined by estimating their proportions. Additionally, the significance of maternal and non-maternal effects as proportions of the reciprocal cross effects was determined. The phenotypic correlations among traits were determined using PROC CORR macros in SAS (SAS-Institute, 2003). Additionally, the contribution of each of the secondary traits towards grain yield was determined using path analysis in SAS.

Heterosis (H) was estimated for grain yield, grain texture, ear aspect, plant and ear heights using data from all the four environments. Both mid-parent (MP) and better-parent (BP) based heterosis were estimated for all the traits following the formulae below (Falconer and Mackay, 1996):

$$\text{MPH} = 100 \times (F_1 - \text{MP})/\text{MP}, \text{ while the } \text{BPH} = 100 \times (F_1 - \text{BP})/\text{BP}$$

Where MPH = Mid-parent heterosis; BPH = Better-parent heterosis; MP = Mean of the two parents involved in a cross; BP = mean of the better parent used in a cross; F_1 = mean of the F_1 hybrid cross.

5.3 Results

5.3.1 Hybrid performance across four environments

Results of the analysis of variance for genotype performance as regards to grain yield, plant height, and ear aspect and grain texture across four environments are shown in Table 5.2. The

results indicated there were highly significant ($P < 0.001$) differences in the four environments for grain yield, plant height, and ear aspect, but there were no significant differences in the environments for grain texture. However, the data were combined for a cross site analysis, because there was a need to compare cultivar performance across sites in order to be able to select stable high yielding hybrids that will ultimately be desired by seed companies and farmers. Regarding genotype performance, the results revealed highly significant ($P < 0.01 - P < 0.001$) differences among genotypes for grain yield and texture. No significant ($P > 0.05$) differences among genotypes were observed for plant height and ear aspect. On the other hand, the interactions environment x genotype were significant ($P < 0.05 - P < 0.001$) for grain yield, grain texture and plant height, but they were not significant for ear aspect.

Table 5.2: Analysis of variance for the performance of 108 genotypes across the four environments in 2011B

Source	DF	Mean Square			
		Grain yield	Plant height	Ear height	Grain Texture
Environment	3	295.02***	161341.35***	11.41***	1.45
Rep(Environment)	4	4.04*	1747.93**	3.01***	3.70***
Genotype	107	77.18***	527.62	0.75	1.13**
Environment*Genotype	321	2.09**	656.54***	0.62	0.89*
Error	428	1.53	435.01	0.62	0.72
Corrected Total	863	3.47	1094.32	0.68	0.85
CV (%)		33.52	11.68	36.51	34.88

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively

5.3.2 Hybrid performance across environments

Results for mean yield and stability of the 20 best and 10 worst performing cultivars across four environments are presented in Table 5.3. The genotype selection index (GSI) ranked the local check 4 (Longe10H) as the best performer in terms of grain yield and stability across environments. However, grain yield of the best seven experimental hybrids was not significantly ($P < 0.05$) different from the best two local checks 4 and 6. The ten poorest performing genotypes across the four environments were significantly ($P < 0.05$) different from the two best performing checks.

Furthermore, the results revealed that parents MV154, MV31, MV44, MV13, MV170 and MV142 were involved in the generation of at least four hybrids each, out of the ten best performing hybrids across the four environments. On the other hand, parents MV21 and MV102 were involved in at least four of the ten worst performing hybrids.

Table 5.3: Mean yield and stability of the top 20 and bottom 10 cultivars across the four environments as ranked by genotype selection index (GSI)

	Genotype	Cross/ genotype	Mean yield (t ha ⁻¹)	IPCA (1)	IPCA (2)	ASV	GSI Rank
Top 20	G104	Longe10H	5.714	0.080	0.108	0.123	1
	G25	MV154 x MV75	5.211	0.040	-0.069	0.073	2
	G36	MV31 x MV170	4.879	0.063	0.232	0.233	3
	G65	MV75 x MV142	4.811	0.063	0.259	0.259	4
	G29	MV31 x MV142	4.662	0.170	0.257	0.281	5
	G106	Longe6H	4.328	-0.092	0.166	0.174	6
	G37	MV44 x MV21	4.207	-0.126	-0.089	0.200	7
	G39	MV44 x MV154	4.629	-0.020	0.291	0.291	8
	G78	MV102 x MV13	4.163	0.093	0.086	0.132	9
	G32	MV31 x MV13	4.215	-0.075	0.173	0.176	10
	G45	MV44 x MV170	5.007	0.245	0.377	0.409	11
	G5	MV21 x MV13	4.065	-0.026	0.062	0.063	12
	G23	MV154 x MV13	4.186	0.068	0.188	0.190	13
	G38	MV44 x MV142	4.412	-0.229	-0.271	0.333	14
	G15	MV142 x MV63	4.124	-0.037	-0.290	0.290	15
	G24	MV154 x MV63	3.887	0.056	-0.115	0.118	16
	G42	MV44 x MV63	4.516	0.104	0.389	0.390	17
	G87	MV170 x MV13	3.872	-0.020	0.094	0.094	18
	G85	MV170 x MV31	4.051	0.141	-0.317	0.323	19
	G30	MV31 x MV154	3.776	-0.004	-0.030	0.030	20
Bottom 10	G81	MV102 x MV170	3.344	0.545	0.406	0.440	99
	G8	MV21 x MV102	3.207	-0.254	-0.080	0.812	100
	G64	MV75 x MV21	3.300	-0.362	-0.127	1.040	101
	G73	MV102 x MV21	3.248	-0.742	-0.151	3.653	102
	G79	MV102 x MV63	3.389	0.611	0.079	4.715	103
	G3	MV21 x MV31	2.432	-0.612	-0.513	0.893	104
	G2	MV21 x MV154	3.624	-1.028	0.254	4.171	105
	G62	MV63 x MV102	3.298	0.568	0.083	3.864	106
	G19	MV154 x MV21	2.959	-0.281	0.050	1.585	107
	G48	MV13 x MV154	2.959	0.432	-0.068	2.757	108
LSD (0.05)			1.600				

IPCA = Interaction principal component analysis, ASV = AMMI stability value, and GSI = genotype selection index

5.3.3 Combining ability effects for grain yield and texture, ear aspect, plant and ear heights

Results of the general combining ability (GCA), specific combining ability (SCA), reciprocal effects (REC), the proportion of reciprocal effects accounted by maternal and non-maternal effects, and environmental interactions towards grain yield, plant and ear height, ear aspect, texture, for 45 experimental hybrids together with their reciprocal crosses and the ten parents across the four environments are presented in Table 5.4.

For grain yield, significant ($P < 0.05$ – $P < 0.001$) mean squares were exhibited for environment, replication, genotype, GCA, SCA, reciprocal and maternal effects; similarly, the interactions between environment and genotype, GCA and environment, and SCA and environment were highly significant ($P < 0.01$ – $P < 0.001$). Conversely, non-maternal effects, and interactions between maternal and non-maternal effects with the environment were non-significant ($P > 0.05$). Regarding the contribution of the genetic effects to hybrid sum of squares, SCA contributed 80.7%, reciprocal effects constituted 13.7%, while the contribution from GCA was 5.6%. For grain texture, only genotypes, SCA and maternal effects were significant ($P < 0.05$ – $P < 0.01$), whereas the environmental, general combining ability, reciprocal, and non-maternal effects, and all interactions were not significant ($P < 0.05$). Similarly, SCA effects had the highest contribution to the hybrid sum of squares with a proportion of 47.0%, followed by reciprocal effects with 41.9%, while GCA contributed 11.1%. Regarding ear aspect, environment, GCA, SCA, and interaction between SCA and environment were significant ($P < 0.05$ – $P < 0.001$), whilst the genotypes, reciprocal effects, maternal and non-maternal effects, and all interactions with environment were not significant ($P > 0.05$) except for the interaction SCA x environment. For the importance of genetic effects, SCA constituted 54.8%, reciprocal crosses had 25.9%, whereas GCA contributed 19.1%.

Table 5.4: Mean squares for grain yield, texture, ear aspect, and the contribution of different genetic effects to the total hybrid sum of squares

Source	DF	Mean square				
		Grain yield (t ha ⁻¹)	Grain texture (score 1-5)	Ear aspect (score 1-5)	Plant Height (cm)	Ear height (cm)
Environment (ENV)	3	285.94***	1.53	9.69***	149297.89***	74071.29***
Rep/ENV [¶]	4	4.63	3.33	2.90	1163.90	295.32
GENOTYPE	99	7.56***	1.09**	0.76	519.23	292.54*
GCA	9	4.62**	1.32	1.61**	470.84	300.19
SCA	45	13.42***	1.13*	0.92*	737.48**	412.10**
REC	45	2.29*	1.01	0.43	310.67	171.46
MAT	9	3.21*	1.69*	0.66	312.09	217.77
NMAT	36	2.06	0.84	0.38	310.32	159.89
ENV*GENOTYPE	297	2.17**	0.83	0.62	648.36***	289.30*
GCA*ENV	27	4.29***	0.93	0.92	1460.37***	667.26***
SCA*ENV	135	2.38**	0.89	1.01***	738.85***	315.22**
REC*ENV	135	1.55	0.74	0.17	395.47	187.79
MAT*ENV	27	1.71	0.64	0.16	380.06	194.64
NMAT*ENV	108	1.51	0.77	0.17	399.32	186.08
R ²		0.78	0.56	0.54	0.80	0.79
CV (%)		34.26	35.38	37.40	11.64	15.65
Hybrids Mean		3.70	2.43	2.13	178.73	80.93
%GCA (SS)		5.55	11.10	19.14	8.24	9.33
%SCA (SS)		80.68	47.00	54.84	64.56	64.03
%REC (SS)		13.76	41.90	25.90	27.20	26.64

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively. ¶: = Replications were nested within environment

On the other hand, the significant effects ($P < 0.05$ – $P < 0.001$) for plant height were: environment, SCA, and the interactions genotype x environment, GCA x environment and SCA x environment. The remaining effects namely genotype, GCA, reciprocal, maternal and non-maternal effects, and the interactions between reciprocal effects, maternal, and non-maternal effects, and the environment were non-significant ($P > 0.05$). Similarly, SCA effects constituted the highest proportion to the hybrid sum of squares with 64.6%, this was still followed by reciprocal effects with 27.2% and GCA had 11.6%. A similar trend was also followed for ear

height, that is, the environment, genotypes, SCA, and interactions between genotype x environment, GCA x environment and SCA x environment. The rest of the factors including GCA, reciprocal maternal and non-maternal effects, and the interactions between reciprocal, maternal and non-maternal effects with the environment were not significant ($P>0.05$). For ear heights, the contribution of SCA effects to the total hybrid sum of squares was 64.0%; the reciprocal effects contributed 26.6%, while GCA effects constituted 9.3%.

5.3.4 General combining ability estimates

Results of the general combining ability (GCA) estimates for grain yield, ear aspect, grain texture, plant and ear heights are presented in Table 5.5. Grain yield results indicated that only parent MV44 had positive and significant GCA estimates ($P<0.05$), while parents MV154, MV31, MV13, MV75, and MV142 exhibited positive but not significant ($P>0.05$) GCA estimates. On the other hand, parent MV21 displayed negative and highly significant ($P<0.01$) GCA estimate, while parents MV63, MV102 and MV170 exhibited negative but not significant ($P>0.05$) GCA estimates. For grain texture, it was only parent MV142 that exhibited positive and significant ($P<0.05$) GCA estimate, parents MV21, MV154, MV44, MV63 and MV75 manifested positive but not significant ($P>0.05$) GCA estimates. Parent MV31 exhibited negative and highly significant ($P<0.01$) GCA values, whereas, parents MV13, MV102 and MV170 displayed negative but not significant ($P>0.05$) GCA estimates for grain texture. In regards to ear aspect, parent MV63 had a positive highly significant ($P<0.01$) GCA value, whilst parents MV154 and MV31 exhibited positive non-significant ($P>0.05$) GCA estimates. The remaining parents MV21, MV44, MV13, MV75, MV102, MV170 and MV142 exhibited negative but not significant GCA estimates for ear aspect.

However, there were no parental lines with significant ($P>0.05$) GCA estimates for plant and ear heights, as the GCA effects for the two traits were not significant in the general analysis of variance for the genetic effects.

Table 5.5: General combining ability (GCA) estimates for ear aspect, grain yield and texture exhibited in the ten parental lines under four environments

Parent	Grain yield (t ha ⁻¹)	Grain texture (Score 1-5)	Ear aspect (Score 1-5)
MV21	-0.368**	0.042	-0.027
MV154	0.034	0.067	0.042
MV31	0.091	-0.193**	0.007
MV44	0.259*	0.029	-0.062
MV13	0.034	-0.080	-0.032
MV63	-0.082	0.048	0.264***
MV75	0.042	0.014	-0.007
MV102	-0.129	-0.011	-0.095
MV170	-0.025	-0.052	-0.051
MV142	0.144	0.136*	-0.039
Standard Errors	±0.132	±0.067	±0.062

*, **, *** indicate the value is significant at P≤0.05, P≤0.01 and P≤0.001, respectively.

5.3.5 Specific combining ability estimates

The specific combining ability (SCA) estimates for grain yield, grain texture, and ear aspect are shown in Tables 5.6, 5.7 and 5.8, respectively. A number of hybrids exhibited significant (P<0.05) SCA estimates for grain yield (Table 5.6). For instance, highly significant (P<0.01 – P<0.001) positive SCA estimates were manifested in all hybrids in which parent MV142 served as a female parent with each of the remaining nine parents serving as a male. On the other hand, in all reciprocal crosses where MV142 served as a male parent the ensuing hybrids displayed both positive and negative non-significant (P>0.05) SCA effects. Other positive and significant SCA effects from the main crosses were displayed in hybrids MV13 x MV21, MV44 x MV154 and MV102 x MV154. SCA effects from other crosses were non-significant. For reciprocal crosses on the other hand, crosses between parents MV21 and MV31, and MV63 and MV75 were negative and significant (P< 0.05). The rest of the hybrids generated from reciprocal crosses displayed non-significant SCA estimates.

Table 5.6: Specific combining ability estimates exhibited for grain yield by hybrids and reciprocals across four environments in 2011B

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		-0.071	0.018	0.244	0.915*	0.403	0.095	0.027	-0.213	1.91**
MV154	0.33		0.50	0.80*	-0.19	0.09	0.30	0.80*	0.01	2.49***
MV31	-1.01*	-0.24		0.04	-0.05	0.17	0.46	0.11	0.70	3.59***
MV44	-0.38	0.16	0.14		0.28	0.34	-0.01	0.29	0.72	2.46***
MV13	-0.21	0.61	0.45	0.17		0.24	-0.30	0.41	0.54	2.50***
MV63	-0.02	0.14	-0.03	0.30	-0.09		0.67	-0.14	0.54	2.50***
MV75	0.17	0.33	-0.27	0.29	-0.58	-0.88*		0.32	0.27	3.76***
MV102	-0.02	0.03	-0.77	0.49	-0.15	-0.05	-0.56		0.04	2.70***
MV170	0.26	0.31	0.41	0.35	0.37	-0.20	0.60	-0.24		2.29**
MV142	0.22	-0.05	-0.10	0.44	0.40	-0.28	-0.04	0.37	-0.13	

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

As far as SCA estimates for grain texture were concerned (Table 5.7), hybrids generated from the main crosses MV21 x MV44, MV21 x MV63, and MV44 x MV170 exhibited positive significant SCA estimates; whereas, crosses MV21 x MV170 and MV44 x MV75 displayed negative significant ($P < 0.05$) SCA estimates. SCA estimates for the rest of the main cross hybrids were non-significant ($P > 0.05$). On the other hand, hybrids from the reciprocal crosses also exhibited some significant SCA values. For example, hybrids from crosses MV154 x MV63 and MV44 x MV170 displayed positive significant ($P < 0.05$) SCA values, while cross MV31 x MV102 exhibited highly significant ($P < 0.001$) negative SCA estimate. SCA estimates for the remaining crosses were not significant ($P > 0.05$).

Table 5.7: Specific combining ability estimates exhibited for grain texture by hybrids and reciprocals across four environments in 2011B

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		-0.25	-0.06	0.44*	0.33	0.39*	0.11	0.11	-0.45*	-0.09
MV154	0.41		-0.21	0.29	-0.01	0.15	-0.16	0.05	0.15	-0.26
MV31	-0.16	0.16		0.40	0.21	-0.15	-0.12	-0.04	0.01	-0.36
MV44	-0.19	0.00	-0.16		-0.03	-0.22	-0.41*	-0.10	0.56**	-0.26
MV13	-0.22	0.09	0.13	0.28		-0.21	-0.27	-0.13	-0.01	0.25
MV63	0.09	0.50*	-0.03	0.09	0.37		-0.02	0.07	-0.02	0.35
MV75	-0.09	-0.16	-0.13	-0.31	-0.09	-0.22		0.13	-0.11	-0.18
MV102	0.19	0.22	-0.75***	0.09	-0.16	0.03	-0.31		-0.05	-0.49
MV170	0.34	0.28	-0.19	0.47*	0.28	-0.16	0.28	-0.13		-0.19
MV142	0.25	0.25	-0.09	0.16	0.28	0.13	-0.19	0.22	-0.19	

*, **, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

Regarding ear aspect (Table 5.8), the cross MV75 x MV170 exhibited highly significant ($P < 0.001$) positive SCA estimates, whereas hybrids MV21 x MV63, MV154 x MV170 and MV63 x MV142 exhibited negative significant ($P < 0.05$ – $P < 0.001$) SCA estimates. For the reciprocal crosses, it was only hybrid MV63 x MV142 that displayed significant positive estimates. The rest of the hybrids had non-significant SCA estimates.

The SCA estimates for plant and ear heights followed a similar trend, with crosses MV21 x MV44 and MV31 x MV142 exhibiting positive and significant ($P < 0.05$) values for both traits, while the rest of the hybrids including the ones from reciprocal crosses did not display significant SCA effects.

Table 5.8: Specific combining ability estimates exhibited for ear aspect by the 45 hybrids and reciprocals across four environments in 2011B

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		-0.20	0.10	-0.01	0.10	-0.41*	-0.02	0.23	-0.03	-0.23
MV154	-0.01		0.03	0.21	0.32	-0.06	-0.02	0.10	-0.37*	-0.39
MV31	-0.14	-0.09		0.07	0.09	-0.08	0.07	-0.03	-0.09	0.10
MV44	-0.05	0.21	-0.12		-0.20	-0.24	-0.05	-0.09	0.11	-0.22
MV13	-0.19	0.33	-0.09	0.20		-0.21	0.01	-0.01	0.13	0.23
MV63	-0.03	0.18	-0.01	0.24	-0.15		-0.28	-0.13	-0.06	-1.22***
MV75	0.01	-0.33	0.03	0.11	0.21	0.06		-0.18	0.64***	0.21
MV102	0.06	-0.14	-0.02	-0.16	0.02	-0.05	-0.03		0.14	0.34
MV170	-0.09	-0.01	-0.01	0.11	-0.03	-0.25	0.18	-0.06		0.33
MV142	0.03	0.09	0.24	0.26	0.28	0.46*	-0.07	0.07	0.25	

*, *** indicate the value is significant at $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively.

5.3.6 Heterosis for grain yield, texture, ear aspect, plant and ear heights

Results for better parent heterosis for grain yield are presented in Table 5.9. Results from both better- and mid-parent (not shown) heterosis revealed good levels were exhibited in grain yield in all experimental hybrids. It ranged from 81.25% and 100.0% to 365.18% and 393.84% for the better- and mid-parent, respectively. The highest better-parent heterosis (365.18%) was registered from hybrid MV75 x MV63; the same hybrid exhibited the highest mid-parent heterosis. Hybrids MV31 x MV170, MV75 x MV31, and MV75 x MV63; and MV102 x MV31, MV142 x MV31, MV102 x MV75, MV75 x MV170, MV31 x MV170, MV75 x MV142, MV75 x MV31, and MV75 x MV63 exhibited heterosis levels above 300% for both better- and mid-parent heterosis. Hybrids MV13 x MV75, MV21 x MV31 and MV13 x MV154 displayed levels of less than 100% for better-parent method, while hybrid MV13 x MV154 displayed the least heterosis of 100% for the mid-parent method. For the rest of the hybrids it fell between 100 and 300%.

Table 5.9: Better parent heterosis (BPH) for grain yield in 45 experimental hybrids and reciprocals across four environments

	MV21	MV154	MV31	MV44	MV13	MV63	MV75	MV102	MV170	MV142
MV21		114.29	241.54	158.28	181.25	182.31	153.85	150.00	117.69	169.23
MV154	158.57		225.71	184.05	87.50	157.14	167.86	212.14	142.86	189.29
MV31	86.92	191.43		142.33	107.50	249.11	310.81	291.38	237.50	278.91
MV44	112.27	204.29	158.90		151.53	139.88	126.99	122.09	163.80	117.18
MV13	153.75	161.88	163.75	172.39		148.75	156.25	160.00	141.88	137.50
MV63	179.23	177.86	242.86	177.30	137.50		365.18	192.24	261.67	221.88
MV75	179.23	215.00	263.06	162.58	81.25	208.04		287.93	182.50	282.81
MV102	146.92	215.43	158.62	182.82	141.25	175.00	190.52		218.33	192.97
MV170	157.69	187.86	307.50	207.36	188.75	202.31	282.50	178.33		195.31
MV142	203.08	182.14	264.06	170.55	187.50	176.92	275.78	253.13	175.00	

5.4 Discussion

5.4.1 Experimental hybrid performance across environments

The significant genotype mean squares observed for grain yield and grain texture revealed differences in performance of the experimental hybrids for the two traits. The non-significant genotype mean squares for plant and ear heights portrayed that hybrids did not display considerable differences in plant and ear heights. The significant environment x genotype interaction mean squares for grain yield, plant height and grain texture revealed considerable differences in experimental hybrid performance across the four environments. This implies that more than one environment is required to evaluate the performance of the experimental hybrids used in the study.

5.4.2 Experimental hybrid performance across environments

The experimental hybrids' performance in regards to grain yield and stability across the four environments indicated that the experimental hybrids were comparable to the local checks. Hybrids selected using genotype selection index (GSI) exhibited good performance for both yield and stability in Masaka (Kamenyamiggo), Serere (NaSARI), and Namulonge (NaCRRI) for season 2011B, and in Namulonge for season 2012A. The mean yields of the best seven hybrids G25, G36, G65, G29, G37, G39, and G32 were 5.2, 4.9, 4.8, 4.7, 4.2, 4.6, and 4.2 (t ha⁻¹), respectively, were not significantly different from Longe10H and Longe6H the best performing checks with yields 5.7 and 4.3 (t ha⁻¹), respectively. The best performing hybrids exhibited small AMMI stability values (ASV) that were comparable to those of the local checks. These results are in agreement with Farshadfar (2008), who indicated that the smaller the AMMI stability values the more stable the cultivars are expected to be across environments. Hybrids G25, G36, G65 and G29 from crosses MV154 x MV75, MV31 x MV170, MV75 x MV142 and MV31 x MV142, respectively, were generated from weevil resistant parental lines (see Chapter Four), therefore, in addition to the good agronomic performance demonstrated, they are expected to exhibit good storability as already manifested by their resistance against weevil infestation.

5.4.3 Combining ability effects for grain yield and secondary traits

The significant environment and genotype mean squares revealed that there were differences in the environments where the genotypes were evaluated. Similarly, the significant genotype indicated considerable differences among genotypes. The significant mean squares for grain yield as manifested by the GCA and SCA effects implied that both additive and non-additive (dominant) gene action were important in the expression of grain yield in the parental lines. However, the higher proportion of SCA sum of squares (80.7%) to total hybrid sum of squares demonstrated that non-additive gene action was more important in governing grain yield compared to additive gene action. The preponderance of non-additive gene action was in agreement with results reported by Machida et al. (2010), who attributed this phenomenon to orientation of the parental inbred lines towards hybrid development. Similarly, Fato et al. (2012) reported significant non-additive gene action from hybridization results of 18 tropical maize inbred lines with ZM523 and Suwan-1 populations under downy mildew infestation.

Furthermore, the significant interactions between environment and genotype for ear aspect, plant and ear heights indicated that considerable variations in genotype performance were

manifested across the four trial environments. Significant GCA effects among secondary traits were only observed for ear aspect, they were not significant in other traits like grain texture, plant and ear height. This observation indicated that additive gene action was important in conditioning ear aspect, but not important in the governance of grain texture, plant and ear height. Conversely, the significant SCA effects observed for grain texture, ear aspect, and plant and ear height portrayed the importance of non-additive gene action in regulating the expression of these traits. The proportion of SCA sum of squares for grain texture, ear aspect, plant and ear height were higher than the GCA and reciprocal sum of squares, indicating that non-additive gene action was more important in the governance of these traits than GCA and reciprocal effects. These results were consistent with those reported by Onwubiko and Onwubiko (2011) who reported significant SCA effects for grain yield, plant height, ear height and ear aspect in hybrids generated from a 12 x 12 diallel cross of maize varieties in Nigeria.

5.4.4 General combining ability for grain yield, grain texture and ear aspect

Results for general combining ability estimates for grain yield, grain texture, and ear aspect showed that parent MV21 displayed a highly significant negative GCA value, signifying a negative contribution towards grain yield. However, parent MV21 was involved in the generation of some of the highest yielding hybrids; therefore, the implication of the negative GCA estimate needs to be understood, as the reasons were not very clear. Parent MV44 on the other hand, exhibited a positive and significant GCA estimate (0.3); indeed exhibited good combining ability in most of its crosses and hence good performance of a number of its hybrids. Three hybrids among the ten best performing hybrids were generated by MV44. Accordingly, the positive GCA value for MV44 and the good performance of a number of its hybrids demonstrated its potential as a good parent for subsequent hybrid development.

For grain texture, parent MV31 manifested a highly significant negative GCA value, due to its contribution towards flint texture in its hybrids; thus MV31 portrayed high potential in generating hybrids with flint texture. On the other hand, parent MV142 displayed a significant positive GCA for grain texture, suggesting that it had considerable contribution towards generating dent hybrids and therefore manifested its potential towards production of dent hybrids. Choice of either parent MV31 or MV44 would depend on the breeding objective of the program. The National maize breeding Program in Uganda prioritizes flint cultivars because they are heavier with a higher milling capacity as compared to the dent varieties, and hence they are more

preferred by farmers and millers. Other breeding programs may prefer dent cultivars because, in addition to ease in milling, they are associated with high grain yield as their kernel arrangement on the cob maximizes space and hence more kernels can be accommodated on a cob. Nevertheless, a balance in the two extremes ought to be achieved, depending on the farmers' and consumers' preferences.

For ear aspect, parent MV63 exhibited positive significant GCA estimate, suggesting that it contributes towards inferior ear aspect, since an increase in ear aspect scores signifies a decline in ear aspect per se.

5.4.5 Specific combining ability for grain yield, grain texture, ear aspect, plant and ear height

Specific combining ability results indicated that parental line MV142 exhibited positive and highly significant specific combining ability effects with the remaining nine parents. Additionally, MV142 was a parent of two of the ten best performing hybrids across the four environments; however, its GCA although positive was not significant. Screening results revealed that MV142 was a good combiner for weevil resistance (see Chapters Three and Four). The outstanding performance of MV142 as a good combiner for both weevil resistance and grain yield demonstrated its potential as a perfect line for use by programs that emphasize weevil resistance; thus it is a suitable candidate for subsequent utilization in grain yield and weevil resistance improvement strategies. Other crosses with positive and significant SCA estimates were MV21 x MV13, MV154 x MV44, and MV154 x MV102. These results suggested that parents MV13, MV21, MV44, MV102 and MV154 would be suitable parents in their respective cross combinations, for generating hybrids with potential for producing high yields.

The significance of the SCA effects among the crosses portrayed the diverse genetic background among the parental lines used in the study; this will provide an opportunity for exploring their genetic potential for hybridization that exploits genetic diversity among germplasm. These results suggested that the three crosses with positive and significant SCA estimates have parents which exhibited reasonable genetic diversity, in addition to parent MV142. Indeed these parents were from different geographical areas; for instance parents MV21 and MV13 were from CIMMYT-Kenya, MV154 and MV142 were from Uganda, while MV63 and MV75 were from the Republic of South Africa.

Results for specific combining ability for grain texture showed significant SCA effects between crosses MV21 x MV44, MV21 x MV63, MV44 x MV170, MV44 x MV170 and MV154 x MV63 suggesting that parents MV21, MV44, MV63, and MV170 exhibited significant contributions towards increased grain texture. Crosses, MV21 x MV170, MV44 x MV75, and reciprocal cross MV31 x MV102 displayed negative and significant SCA estimates implying they contributed significantly to an increase in grain flintiness; thus they are candidate parents for breeding for increased flintiness in hybrids. For ear aspect, crosses MV21 x MV63, MV154 x MV170 and MV63 x MV142 that manifested negative significant SCA values were significantly contributing to increased ear aspect, whereas cross MV75 x MV170 and reciprocal cross MV142 x MV63 were exhibited significant reductions in ear aspect. Additionally, from the SCA results it was observed that the main cross MV63 x MV142 displayed highly significant negative SCA value (-1.2***) whereas it's reciprocal MV142 x MV63 exhibited significant positive SCA value (0.5*). This is a clear observation of reciprocal effects; although the whole sample analysis did not portray significant reciprocal effects there were a few crosses that displayed reciprocal effects.

5.4.6 Better parent heterosis for grain yield

Heterosis was estimated using both better and mid-parent methods and was highly exhibited in grain yield and other traits, for most of the experimental hybrids. Results from the better parent method indicated that high heterosis levels were exhibited in the experimental hybrids. The highest level was 365.2% displayed between parents MV75 and MV63; the same cross displayed the highest mid-parent heterosis level. A part from cross MV75 x MV63 that comprised of parents from the same origin (southern Africa), most of the crosses that exhibited heterosis levels above 200.0% were between parents from different germplasm sources. For example, parent MV31 from CIMMYT-Kenya exhibited heterosis levels of 249.1%, 310.8%, and 291.4% with parents MV63, MV75 and MV102, respectively from Uganda, in addition to 237.5% and 278.9 with parents MV170 and MV142, respectively from South Africa. Since high levels of heterosis are usually manifested between individuals of diverse genetic background, the high heterosis levels exhibited in the experimental hybrids suggested wide genetic diversity between maize germplasm from Uganda, CIMMYT-Kenya and South Africa, and this could be exploited for future hybrid development and ultimately yield enhancement. There were good levels of heterosis from crosses between parents MV75 x MV63 and MV75 x MV102 that is 271.0% and 275.0%, respectively and this suggested that there was still high genetic diversity within the southern Africa maize germplasm lines, which could still be exploited for enhancing maize yields

through hybridization. The high heterosis levels further demonstrated the importance of non-additive gene action in the governance of grain yield. These results were in agreement with Makumbi et al. (2011) who reported heterosis levels of over 500.0% from studies on drought- and nitrogen-stress.

5.5 Conclusion

The results indicated that eastern and southern Africa maize germplasm lines can act as parental lines for hybrid development. Parental line MV44 from CIMMYT-Kenya exhibited positive and significant general combining ability (GCA) effects that can be useful for further studies focusing on its use for generation of hybrids and synthetics.

The high proportion of the SCA sum of squares together with the manifestation of high levels of heterosis in various hybrids portrayed the preponderance of non-additive gene action towards the governance of grain yield in the parental lines. Thus, grain yield would be enhanced mainly through hybridization.

The high heterosis levels manifested in the majority of crosses revealed the high genetic diversity that ought to be exploited further for yield and maize weevil resistance enhancement through hybridization, especially between crosses MV170 and MV75, MV142 and MV75, MV170 and MV102, MV170 and MV44, and MV170 and MV31 in which high levels of heterosis were exhibited.

The comparable performance of some experimental hybrids to the local checks over the four environments demonstrated the potential of these hybrids in outcompeting the current commercial cultivars. The experimental hybrids are expected to exhibit enhanced levels of resistance to the maize weevil against which their parents had been selected. Hence subsequent utilization of elite germplasm identified from this study would have a major contribution towards enhancing maize productivity and grain storability.

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Chapter Six

Response of maize population “Longe5” to two cycles of modified S₁ recurrent selection for resistance to maize weevil.

Abstract

The maize weevil (*Sitophilus zeamais* Mostchulsky) is one of the most important storage pests causing significant reductions in grain weight and quality in tropical and subtropical regions. The current study determined the effectiveness of two cycles of modified S₁ recurrent selection towards the improvement of weevil resistance in Longe5. Grain yield and resistance to *Turcicum* leaf blight (TLB), grey leaf spot (GLS) and rust were also considered to enhance the overall worth of the variety. Selections were made by identifying and selfing foliar disease resistant, vigorous plants, with potentially big well-placed ears from a Longe5 maize population (cycle C₀), grown at the National Crops Resources Research Institute, Namulonge, in Uganda. Over 540 selfed ears were obtained from cycle C₀ and screened for weevil resistance in the laboratory at Namulonge, after which 162 weevil resistant genotypes were selected and recombined in an isolated field to generate cycle C₁. Cycle C₂ was generated from cycle C₁ in a similar procedure, by recombining 190 weevil resistant cycle C₁ genotypes. Cycles C₀, C₁, and C₂ were evaluated for yield and reaction to foliar diseases at three locations and the ensuing seed was screened for maize weevil resistance in a randomized complete block design. Results for weevil resistance indicated a reduction in grain weight loss of 64.7% registered in C₂, whereas in C₁ a decline of 15.0% was registered. For F₁ weevil progeny emergence, C₂ exhibited a reduction in weevil number of 33.4%, while C₁ reduced by 18.6%. The reduction in kernel damage was 63.4% in C₂, whereas in C₁ it was reduced by 33.6%. Grain yield results indicated a yield gain of 29.7% realized between cycles C₂ and C₀, a yield gain of 11.6% realized between cycles C₂ and C₁, while a yield gain of 16.2% was realized between cycles C₁ and C₀. Reductions in disease severity of 26.7%, 10.2% and 12.5% were exhibited for TLB, GLS and rust, respectively, in cycle C₂. The results suggested that Longe5 can be improved for weevil resistance, grain yield, and resistance to foliar diseases through modified S₁ recurrent selection. Hence further recurrent selection cycles would be recommended.

Key words: Disease resistance, grain yield, Longe5, maize, selection gain, weevil resistance.

6.1 Introduction

The maize weevil (*Sitophilus zeamais* Mostchulsky) is one of the most destructive storage insect pests of maize in all maize growing zones in tropical and subtropical ecosystems worldwide. Weevil infestation is encountered both at on-farm level and at traders' level where it causes huge loss in grain weight in addition to deterioration in quality (Giga et al., 1991). Furthermore, weevil infested maize has been associated with frequent attack by ear rot pathogens and subsequently mycotoxins (Sone, 2001; Kaaya et al., 2005). With the increasing demand for maize in the eastern Africa regional market, quality assurance would be paramount for enhancing maize marketability (Magnay, 2004). Effective control of the maize weevil would greatly improve its market quality, and quantity to a great extent. Although use of chemicals is one of the most common control strategies, chemicals are expensive to smallholder farmers and environmentally undesirable. Grain resistance is one of the most sustainable control measures against the maize weevil and a major component of integrated pest management, which is cheaper and safer ecologically (Abebe et al., 2009; Tefera et al., 2011a). Weevil resistance has been identified in various maize germplasm (Widstrom et al., 1983; Li et al., 1998; García-Lara et al., 2009; Dari et al., 2010; Mwololo et al., 2012). However, introgression of weevil resistance and deployment of weevil resistant maize cultivars is still limited in Uganda and elsewhere in tropical and subtropical environments where such maize is in demand.

Recycling of seed from one season to another is still a popular practice in sub-Saharan Africa due to the high seed cost and limited access to quality seed (Sserunkuuma, 2003; De Groote et al., 2010). Farmers have shown preference for the variety Longe5 because of its quality protein nature, easy access to seed, and high adaptability (De Groote et al., 2010). For the same reasons, a number of projects have been implemented to promote Longe5, especially in schools and resettlement schemes in northern Uganda where they are rehabilitating people formerly affected by the war. However, Longe5 is susceptible to the maize weevil and a number of foliar diseases. Therefore, its improvement for weevil resistance, yield and resistance to the major foliar diseases, especially, *Turcicum* leaf blight (*Exserohilum turcicum*), grey leaf spot (*Cercospora zea* maydis), and rust (*Puccinia sorghi*) would enhance its productivity and storability. This will contribute towards improving food, nutrition and income security of smallholder maize farmers in Uganda and beyond. Recurrent selection increases the frequency of desirable genes in maize gene pools (Hallauer and Miranda, 1988). In the same regard, the frequency of genes conditioning weevil resistance in maize can be increased through selection

(Van Schoonhoven et al., 1975). Dhliwayo and Pixley (2003) registered significant reductions in grain weight loss, weevil progeny emergence and Dobie index of susceptibility in synthetics generated through divergent selection among S_1 and S_2 lines derived from six maize populations. As regards to yield, Badu-Apraku et al. (2009) reported up to 58% increase in grain yield per cycle of S_1 recurrent selection in maize under *Striga*-free and *Striga*-infested environments. However, there are no studies that have emphasized concurrently selection for both maize weevil resistance and agronomic performance.

The current study was conducted to determine the effectiveness of two cycles of selection in improving grain resistance against weevil damage, grain yield, and resistance to the major foliar diseases in Longe5. Improved resistance against weevil damage would enhance its storability and utilization. The study objectives were to i.) determine the possible gain in weevil resistance in Longe5, ii) determine the potential gain in grain yield and secondary traits, and iii) determine the improvement in resistance against foliar diseases (grey leaf spot, *Turicum* leaf blight and rust) after two cycles of modified S_1 recurrent selection. The study was performed with a view to recommend further selection and devising the appropriate breeding strategy for programs that seek to emphasize value for grain cultivation and storage in tropical maize.

6.2 Materials and methods

The study was conducted between September 2009 and November 2012, during when two selection cycles (C_1 and C_2), were generated from the source population (C_0) of Longe5 using S_1 recurrent selection, modified by selfing only once at the beginning of the selection process. Individuals in the subsequent cycles (C_1 and C_2) of selection were not selfed, due to time constraint.

6.2.1 Experimental sites

Genotype screening for weevil resistance and generation of the three selection cycles C_0 , C_1 , and C_2 (populations) was done at the National Crops Resources Research Institute (NaCRRI), Namulonge, Uganda (0°32'N, 32°34'E, 1200 m.a.s.l.). Field evaluation of the performance of the three selection cycles was done at Namulonge; Masaka District Agricultural Training and Information Centre (DATIC), Kamenyamiggo (0°18' 18.2" S, 31°39'50.1" E, 1253 m.a.s.l.); and the National Semi-Arid Resources Research Institute, Serere (1° 32'N, 33°27'E, 1140 m.a.s.l.).

6.2.2 Experimental materials

An open pollinated quality protein maize (QPM) variety, Longe5, was used as the source population from which S_1 genotypes and cycles C_1 and C_2 were derived.

6.2.3 Generation of Longe5 S_1 population

The source population of Longe5 was planted in isolation at Namulonge in September 2009. Towards silking, in mid-November, over 1000 genotypes were selected and tagged for subsequent selfing. The selection criteria were vigorous growth, freedom from stem and root lodging, potentially big well placed ears, and low disease scores (≤ 2 on a 1 to 5 scale) for *Turcicum* leaf blight, grey leaf spot, and rust. Selfing was done to enhance accumulation of desired genes. At physiological maturity (January 2010), a representative number of ears (about 500) was harvested from the unselfed genotypes, shelled, and thoroughly mixed for obtaining a sample of grain that was used as cycle zero (C_0). On the other hand, over 1000 selfed ears were individually shelled and examined for QPM characteristics. At all selection stages, a light table was used to identify ears with the modifier gene expression (with waxy endosperm) that is characteristic for QPM maize genotypes (Vivek et al., 2008). Consequently, 540 S_1 ears exhibiting appropriate QPM characteristics (modification classes 2 and 3) were selected and their kernels divided into two batches as follows: i) the first batch (75 g) was prepared for laboratory screening against weevils at Namulonge, and ii) the second batch (10 to 15 g) was planted for seed multiplication, and subsequent selection and cycle advancements.

6.2.4 Laboratory screening of the source population for weevil resistance

The grain for screening against weevils was first subjected to cold treatment in a deep freezer at -20°C for 14 days to kill any weevils already in the seed after which it was acclimatized to the laboratory conditions for one week. Each sample for screening against weevils was then divided into three replications (each weighing 25 g) and placed into glass jars of 250 ml. The moisture contents of the samples were ranging from 12.0 to 15.0%. Towards the end of February 2010, thirty two young adult weevils of 0 – 7 days old (previously reared within the same laboratory) were introduced into glass jars covered with perforated lids, to allow proper ventilation. Small wire meshes of pore size <1 mm were fitted in the perforated lids to prevent weevil escape. The maize-weevil culture was incubated at a temperature of $28 \pm 2^\circ\text{C}$ and relative humidity of $70 \pm 5\%$, a heater fan and a humidifier were used to maintain these conditions. After 75 days the cultures

were examined for genotypic response to weevil infestation. The grain susceptibility parameters used for assessing genotypic response to weevil infestation were: grain weight loss, total number of live and dead weevils (weevil mortality) and percent grain damage, calculated according to Tefera et al. (2011). The best 162 genotypes were selected and their corresponding rows identified in the field for recombination.

6.2.5 Seed multiplication

To save on time, preliminary genetic recombination, seed increase, and laboratory screening of the 540 S₁ genotypes for weevil resistance were carried out simultaneously in 2010A. One 5 m-row plot of each genotype was planted in March 2010, the intra-row spacing was 0.3 m, and thus an average of 14 plants was raised for each S₁ genotype. Based on the laboratory results on genotypic response to weevil infestation, 162 weevil resistant S₁ genotypes were selected and tagged in the field. At flowering, the silks of the selected genotypes were shoot-bagged and their tassels covered to eliminate pollen contamination from other genotypes. Genetic recombination among selected genotypes was effected by collecting, bulking, and thoroughly mixing their pollen daily, and uniformly pollinating receptive silks. A scale of 1 to 5 was used to select genotypes for pollination. Pollinations were only carried out among genotypes without or minimal manifestations of foliar diseases (scores <2.0). At dry maturity, pollinated genotypes were harvested, dried and shelled in bulk. The grains were then thoroughly mixed to ensure uniformity and it was then stored as seed for planting in the subsequent season (2010B).

6.2.6 Genetic recombination

In the second rainy season of September 2010 (2010B), the seed obtained from the first season (2010A) was used to plant 0.5 ha of the selected genotypes for genetic recombination at Namulonge. The seed of weevil resistant genotypes was uniformly mixed and randomly planted in an isolation block to enhance random out-crossing and hence genetic recombination among genotypes, for generation of cycle one (C₁) population. Before flowering, all undesirable plants with high disease severity and poor agronomic characteristics were de-tasseled and their ears were not harvested for advancement, this was to ensure that inferior genotypes were reduced from the gene pool. To avoid contaminations with undesired genes from other maize populations, an isolation distance of a minimum of 700 m to the next maize crop was observed. Superior genotypes in terms of disease resistance and agronomic traits (good ear placement,

plant and ear aspects) were identified and tagged before drying. At maturity, at least 1000 ears from intact plants (not detasseled) were harvested, shelled and examined for QPM characteristics on a light table.

6.2.7 Production of seed for evaluation trial

A total of 600 cycle one (C_1) ears with QPM characteristics were simultaneously screened for weevil resistance and planted in the field in 2011A for seed increase. Out of the 600 genotypes screened, 190 most weevil resistant genotypes (about 30%) were selected and their pollen collected, bulked and pollinated to all receptive silks of the selected genotypes. The pollinated ears were covered with pollination bags to avoid pollen contaminations from unselected genotypes. The resulting seed was planted in an isolation block in 2011B, to allow genetic recombination among genotypes; this resulted in the generation of cycle two (C_2) population. At the same time, C_0 and C_1 populations were each planted in isolation in 2011B, for purposes of producing new seed lots with the same grain characteristics as that of the newly recombined cycle two (C_2) kernels. At maturity (January 2012), seed from the three populations (C_0 , C_1 , and C_2) was harvested and prepared for an evaluation trial in 2012A (first rainy season of 2012).

6.2.8 Field trial establishment, yield and secondary traits assessment

Seed from the three populations namely C_0 , C_1 , and C_2 was harvested in January 2012 and prepared for planting in a multi-location trial at Namulonge, Masaka and Serere. The trial was planted in a randomized complete block design with six replications. Three 5 m - row plots were used per replication per cycle, with a spacing of 0.75 m between rows, and 0.3 m between plants thus giving a total plant population of 44,444 plants per ha. Di-ammonium phosphate (18% P) and Urea (46% N) were added at the rate of 33 kg P and 120 kg N per hectare, respectively. The trials were maintained weed free by hand weeding. To eliminate out-crossing among the three cycles, controlled pollination using bulked pollen from within each replication was done on at least 30 plants per replication for each cycle. Assessments for foliar diseases were carried out as described in Chapter Three, section 3.2.3. Yield estimations and secondary trait assessments were conducted as in Chapter Five, section 5.2.1.

6.2.9 Laboratory evaluation of C₀, C₁, and C₂ populations for weevil resistance

Grain samples were collected from each cycle at each site. Each field replicate was represented by one glass jar, thus the screening trial was also replicated six times (as it was done for the field evaluation trial). Therefore, 18 glass jars were generated from each location, giving a total of 54 glass jars that were evaluated in the laboratory. The culture conditions and procedure used for weevil rearing and maize screening were as described in Chapter Three sections 3.2.5 and 3.2.6, respectively. Maize grain of weight 50 g was put in 250 cm³ glass jars and infested with 50 adult weevils of 0 to 7 days old. The maize-weevil cultures were laid out in the laboratory in a randomized complete block design. The grain susceptibility parameters used for assessing the response of the three cycles to weevil infestations were: total number of F₁ weevil progeny emergence, weevil mortality, percent grain-weight loss, and percent grain damage. Percent grain weight loss and damage were calculated according to Tefera et al. (2011).

6.2.10 Data analysis

The data obtained were subjected to general linear model program (SAS-Institute, 2003). The means for all study parameters were separated and the least significant difference determined. The model used for the estimation of the grain susceptibility parameters were:

Response to weevil infestation: $Y_{ijk} = \mu + E_i + R_j + C_k + EC_{ik} + e_{ijk}$

Where Y_{ijk} = observed value of the trait; μ = overall mean of the trait; E_i = effect of the i^{th} site/environment ($i = 1, 2, 3$); R_j = effect of the j^{th} replication ($j = 1, 2, 3, 4, 5, 6$); C_k = effect of the k^{th} cycle ($k = C_0, C_1, C_2$); EC_{ik} = effect of the interaction of the k^{th} cycle in the i^{th} site; e_{ijk} = residual effect.

The model used for estimation of yield and secondary traits performance, and response to foliar diseases was: $Y_{ijkl} = \mu + E_i + P(R^*E)_{ij} + C_k + EC_{ik} + e_{ijkl}$

Where Y_{ijkl} = observed value of the trait; μ = overall mean of the trait; E_i = effect of the i^{th} site/environment ($i = 1, 2, 3$); $P(R^*E)_{ij}$ = effect of the l^{th} plot in the j^{th} Replication ($j = 1..6$), under the i^{th} site/environment; C_k = effect of the k^{th} cycle ($k = C_0, C_1, C_2$); EC_{ik} = effect of the interaction of the k^{th} cycle in the i^{th} site; e_{ijkl} = residual effect.

To determine the correlations between the various study parameters, the SAS Procedure “PROC CORR” was performed (SAS-Institute, 2003).

The selection gain was calculated according to the method described by Keeling (1982), as:

$$\text{Selection gain} = \frac{\text{Performances of advanced population} - \text{Performances of original population}}{\text{Performances of original population}} \times 100$$

6.3 Results

6.3.1 Grain response to artificial infestation with the maize weevil

Mean squares for grain response to weevil infestations exhibited by grain weight loss, F₁ weevil progeny emergence, weevil mortality and kernel damage in the three selection cycles grown at Namulonge, Masaka, and Serere in 2012A are shown in Table 6.1. For grain susceptibility parameters grain weight loss and kernel damage, their mean squares indicated that only cycles were significant (P<0.01 – P<0.001). For F₁ weevil progeny emergence, sites, cycles and the interactions between site x cycle were significant (P<0.05 – P<0.001), whereas for weevil mortality none of the effects were significant (P>0.05).

Table 6.1: Mean squares for grain weight loss, live weevils, weevil mortality, and kernel damage exhibited in grain obtained from cycles C₀, C₁ and C₂

Source	DF	Mean Squares			
		FWE	GWL	WM	KD
Site	2	2081.80**	0.25	80.30	113.04
Rep	5	2103.49	8.011	1010.29	235.32
Cycle	2	1718.91**	29.79**	23.35	1718.93***
Site*Cycle	4	713.77*	5.01	59.29	193.89
Error	40	264.04	3.63	71.91	92.98
R ²		0.67	0.51	0.66	0.601
CV (%)		9.37	51.1	20.11	46.28

*, **, *** indicate significance at 0.05, 0.01, and 0.001 probability levels. FWE = F₁ weevil progeny emergence; GWL = Grain weight loss; WM = Weevil mortality; KD = Kernel damage (%).

Results of the response to weevil infestation of the grain obtained from cycles C₀, C₁, and C₂ grown at Namulonge, Masaka, and Serere in 2012A are presented in Table 6.2. The results indicated no significant differences (P>0.05) in grain weight loss, weevil mortality, and kernel damage among the three sites. However, significant differences were exhibited in F₁ weevil

progenies, whereby, grain obtained from Masaka manifested a significantly ($P < 0.05$) higher mean for F_1 weevil progenies emerging than the grain from Namulonge and Serere.

Table 6.2: performance of the three cycles across three locations in 2012A as reflected in grain response to grain susceptibility parameters

Site	Grain susceptibility parameters			
	FWE	GWL	WM	KD
Namulonge	41.67	5.32	21.28	19.84
Masaka	60.72	5.79	19.28	23.69
Serere	42.56	5.61	23.5	18.99
LSD (0.05)	10.95	2.57	ns	6.5

ns = not significant. FWE = F_1 weevil progeny emergence; GWL = Grain weight loss (%); WM = Weevil mortality; KD = Kernel damage (%).

6.3.2 Selection gain in weevil resistance

Results of the response of the three cycles (C_0 , C_1 , and C_2) to artificial weevil infestation as revealed by grain weight loss, F_1 weevil progeny emergence, weevil mortality and kernel damage in C_0 , C_1 , and C_2 are shown in Table 6.3. The results indicated significant differences between the source population (C_0) and the two selection cycles for grain weight loss, F_1 weevil progeny emergence and kernel damage. The mean number of F_1 weevil progenies that emerged from C_2 grain was 39 weevils, which was significantly lower than the 58 F_1 weevils that emerged from C_0 seed. The F_1 weevil emergence from C_1 seed was not significantly different from C_0 , neither was it significantly different from C_2 (it fell between the two cycles). For grain weight loss, cycle C_2 encountered significantly lower grain weight loss (2.6%) than cycles C_0 (7.6%) and C_1 (6.5%) which were not significantly different from one another. For percent kernel damage, C_2 seed registered the lowest damaged of 11.3%, which was significantly lower than C_1 (20.5%), which in turn was significantly lower than C_0 . Regarding weevil mortality, there were no significant differences among the three seed cycles.

Table 6.3: Selection gain exhibited in the three cycles of selection as reflected in grain response to grain susceptibility parameters

Cycle	Weevil susceptibility parameter			
	FWE	GWL	WM	KD
C ₀	58.44	7.59	20.67	30.8
C ₁	47.56	6.45	22.67	20.46
C ₂	38.94	2.45	20.72	11.26
LSD (0.05)	10.95	2.57	ns	6.5

FWE = F₁ weevil progeny emergence; GWL = Grain weight loss (%); WM = Weevil mortality; KD = Kernel damage (%); ns = not significant at P = 0.05.

Results of percentage gains in selection exhibited among the three cycles, as portrayed by the four susceptibility parameters are presented in Figure 6.1. The selection gains in the weevil susceptible parameters: F₁ weevil progeny emergence, grain weight loss and percent kernel damage were manifested as reductions in magnitude of their expressions. Therefore, for F₁ weevil progeny emergence, the mean number of progenies emerging from the grain dropped by 18.6% on advancement from C₀ to C₁, a drop in F₁ weevil progeny emergence of 33.4% was observed between cycles C₀ and C₂, while an 18.1% decline was observed between C₂ and C₁. For grain weight loss, a decline in loss of 15% was exhibited between C₁ and C₂, a 64.7% decline was observed between C₂ and C₀, while a 58.5% decline was displayed between C₂ and C₁. Similarly, for kernel damage a reduction in damage of 33.6% was exhibited between C₁ and C₀, a reduction of 63.4% was observed between C₂ and C₀, while a 45.0% reduction in kernel damage was displayed between C₂ and C₁. For weevil mortality on the other hand, insignificant increments were observed among the three cycles.

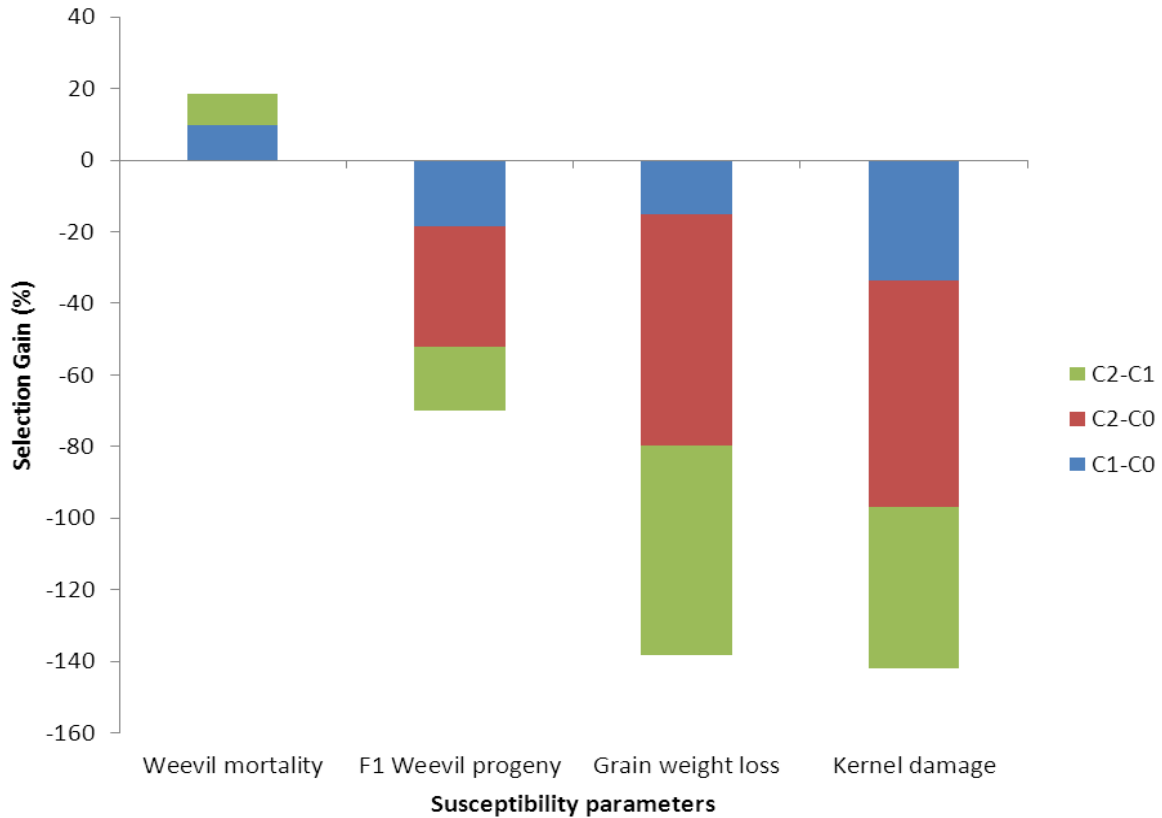


Figure 6.1: Percentage selection gain for grain susceptibility parameters exhibited among cycles

6.3.3 Correlations between grain weight loss, live weevils, weevil mortality, and kernel damage

Results of the correlations between the four grain susceptibility parameters are shown in Table 6.4. The results indicated positive significant ($P < 0.01$ – $P < 0.001$) correlations between grain weight loss and live weevils, and between grain weight loss and kernel damage. The correlation between weevil mortality and the other parameters was not significant ($P > 0.005$) although negative.

Table 6.4: Correlation of grain susceptibility parameters

	Grain weight loss	Live weevils	Weevil mortality	Kernel damage
Grain weight loss				
Live weevils	0.42**			
Weevil mortality	-0.25	-0.57***		
Kernel damage	0.46***	0.51***	-0.25	

, **, *** indicate significance at 0.05, 0.01, and 0.001 probability levels.

6.3.4 Field performance of the two selection cycles as reflected in grain yield, grain texture, ear aspect, and response to foliar diseases

Mean squares for yield, grain texture, ear aspect, TLB, GLS, and rust are shown in Table 6.5. The means squares for yield, ear aspect, TLB and GLS indicated that sites were highly significant ($P < 0.001$), while grain texture and rust mean squares indicated sites were not significant ($P > 0.05$). Cycles were highly significant ($P < 0.01 - P < 0.001$) for all traits; whereas it was only grain texture which exhibited highly significant ($P < 0.01$) interactions between site and cycle, the rest of the traits did not display any significant ($P > 0.05$) interactions.

Table 6.5: Mean squares for grain yield, grain texture, ear aspect and response to foliar diseases exhibited in cycles C₀, C₁ and C₂ at three locations in 2012A

Source	DF	Mean squares					
		Yield (t ha ⁻¹)	GT (Score1–5)	EA (Score 1–5)	TLB (Score 1–5)	GLS (Score 1–5)	Rust (Score 1–5)
Site	2	51.85***	0.26	5.40***	5.75***	1.83***	0.06
Plots(Site*Rep)	51	0.92	0.22	0.24	0.20	0.08	0.15
Cycle	2	23.09***	2.87***	6.77***	7.16***	0.76**	0.80***
Site*Cycle	4	0.12	0.92**	0.18	0.24	0.07	0.06
Error	102	1.10	0.24	0.23	0.26	0.12	0.10
R ²		0.64	0.47	0.61	0.59	0.42	0.48
CV (%)		13.83	20.73	20.18	22.25	18.53	19.08

, * indicate significance at 0.01 and 0.001 probability levels. GT = grain texture, EA = ear aspect, TLB = *Turicum* leaf blight, GLS = grey leaf spot.

6.3.5 Cycle performance across sites reflected in grain yield, texture, ear aspect, and response to foliar diseases

Results of the mean performance of cycles C_0 , C_1 , and C_2 in Namulonge, Masaka, and Serere are presented in Table 6.6. Grain yield results indicated that the three sites were significantly different ($P < 0.05$) as regards to the performance of the three cycles. Grain yield was highest at Namulonge with a mean of 4.6 t ha^{-1} , followed by Serere with a mean of 4.1 t ha^{-1} , and then Masaka with a mean yield of 3.5 t ha^{-1} . For grain texture, there were no significant differences exhibited across sites; while for ear aspect, Namulonge and Serere exhibited significantly better ear characteristics with a mean score of 2.2, than Masaka which displayed a mean score of 2.7. Regarding response to foliar diseases, there were no significant differences ($P > 0.05$) among the three sites towards rust disease. For TLB, it was significantly more manifested in Masaka, than in Namulonge and Serere; whereas, for GLS, Namulonge exhibited significantly lower scores than Masaka and Serere.

Table 6.6: Mean performance of the three cycles across three sites in 2012A as reflected in grain yield, texture, ear aspect and responses to *Turcicum* leaf blight, grey leaf spot and rust

Site	Grain yield (t ha^{-1})	Texture (Score 1-5)	Ear aspect (Score 1-5)	TLB (Score 1-5)	GLS (Score 1-5)	Rust (Score 1-5)
Namulonge	4.58	2.38	2.18	2.07	1.69	1.66
Masaka	3.52	2.42	2.74	2.65	2.01	1.71
Serere	4.14	2.29	2.20	2.09	2.02	1.72
LSD (0.05)	0.42	ns	0.16	0.18	0.12	ns

TLB = *Turcicum* leaf blight and GLS = grey leaf spot.

The results for the mean performance of cycles C_0 , C_1 , and C_2 as regards to grain yield, grain texture, ear aspect, and response to TLB, GLS, and rust are presented in Table 6.7. Significant differences were exhibited among cycles for all traits. Results of grain yield showed that cycle C_2 with mean grain yield of 4.8 t ha^{-1} , significantly outperformed cycle C_1 (4.2 t ha^{-1}), which in turn outperformed cycle C_0 (3.4 t ha^{-1}). The same trend was manifested for grain texture, whereby C_2 exhibited the smallest, and relatively the most, desirable mean score of 2.1, followed by C_1 with a mean score of 2.4, and lastly C_0 with a mean score of 2.6. For ear aspect, C_2 exhibited a mean score of 1.9 that was significantly better than C_0 with a mean score of 2.5 and C_1 with a mean score of 2.7. As regards to response to TLB, the three cycles were

significantly different from one another, with C₁ displaying the lowest mean score (1.9), followed by C₂ (2.2) and lastly by C₀ (2.7). For GLS, C₂ exhibited a significantly lower score of 1.8 than C₁ and C₀ that exhibited the same scores of 2.0. For rust on the other hand, cycles C₂ (1.6) and C₁ (1.6) were not significantly different (P<0.05) from one another, but were significantly better than C₀ (1.8).

Table 6.7: Selection gain exhibited of the three cycles of selection as reflected in grain yield, texture, ear aspect and responses to *Turcicum* leaf blight, grey leaf spot and rust across three locations in 2012A

Cycle	Grain yield (t ha ⁻¹)	Texture (Score 1-5)	Ear aspect (Score 1-5)	TLB (Score 1-5)	GLS (Score 1-5)	Rust (Score 1-5)
C ₀	3.44	2.56	2.48	2.66	2.00	1.84
C ₁	4.20	2.42	2.67	2.20	2.00	1.64
C ₂	4.82	2.11	1.98	1.95	1.80	1.61
LSD (0.05)	0.42	0.16	0.16	0.18	0.12	0.11

TLB = *Turcicum* leaf blight and GLS = grey leaf spot.

Results for the gain in selection exhibited in grain yield and other traits are shown in Figure 6.2. Grain yield results indicated a selection gain of 29.7% (1.1 t ha⁻¹) observed between C₂ and C₀, a gain of 11.6% (0.5 t ha⁻¹) was exhibited between C₂ and C₁, while the selection gain observed between C₁ and C₀ was 16.2% (0.6 t ha⁻¹). For grain texture, a gain in selection of -5.5% was exhibited from C₀ to C₁, a gain of -12.8% was displayed between C₂ and C₁, while a gain of -17.58% was displayed between C₀ and C₂. For ear aspect, a decline in performance of 5.7% was observed from C₀ to C₁, while gains of -20.2% and -25.8% were exhibited between C₂ and C₀, and C₂ and C₁, respectively. As regards to GLS, a decline in resistance was observed from C₀ to C₁ while selection gains of -10.2% and -10.6% were registered between C₂ and C₀, and C₂ and C₁, respectively. The gains in selection were -10.9% and -12.5%, exhibited between cycles C₁ – C₀, and C₂ – C₀, respectively. The gain between C₂ and C₁ was -1.8%.

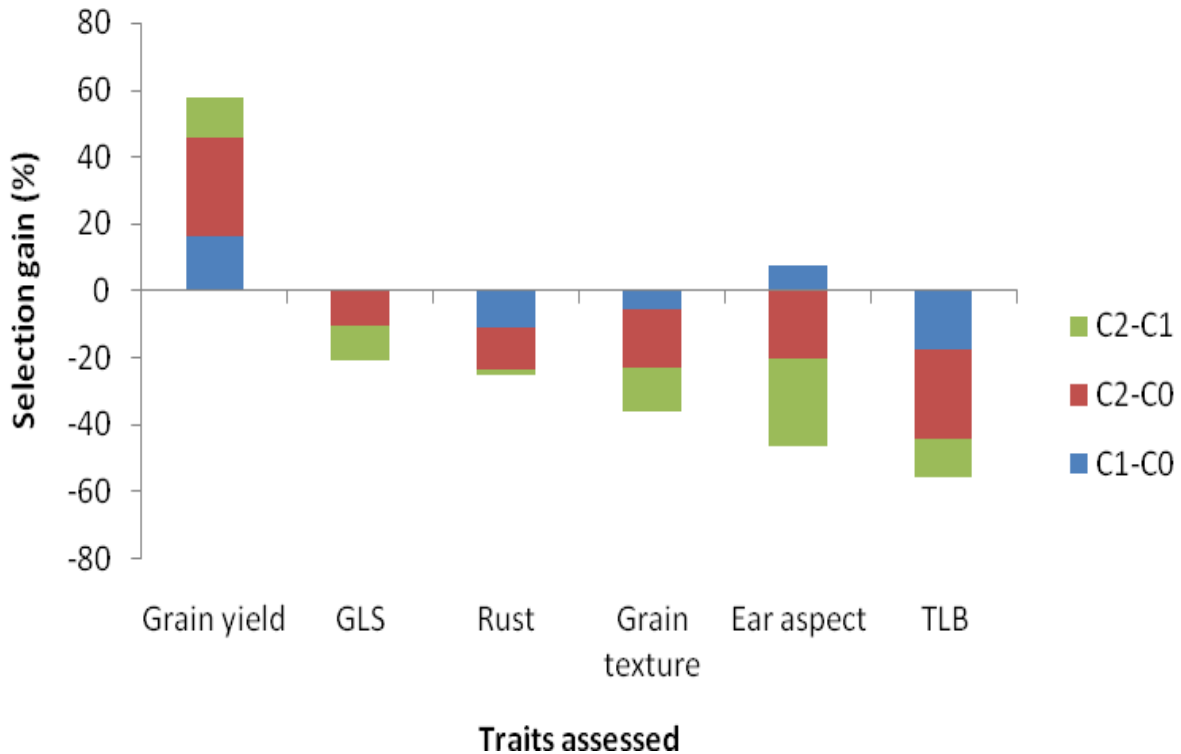


Figure 6.2: Percentage selection gain exhibited among the three cycles across three sites for grain yield and other traits in Longe5.

6.3.6 Correlations between study parameters

The correlations between grain yield, grain texture, ear aspect, GLS, rust, and TLB are shown in Table 6.8: The results revealed that all study parameters were negatively correlated to yield; with grain texture, GLS, TLB, and ear aspect being significant ($P < 0.05$ – $P < 0.001$) and negatively correlated to yield, while the correlation between rust and yield was negative but not significant ($P > 0.05$). Other significant correlations were positive; for instance the correlation between grain texture and TLB was positive and significant ($P < 0.05$), the correlation between ear aspect and TLB was positive and significant ($P < 0.001$); similarly, a positive and significant ($P < 0.01$) correlation was observed between rust and TLB.

Table 6.8: Correlations between grain yield, grain texture, ear aspect, grey leaf spot (GLS), rust, and *Turcicum* leaf blight (TLB)

	Grain texture	GLS	Rust	TLB	Ear aspect	Grain yield
Grain texture						
GLS	0.02					
Rust	0.01	0.09				
TLB	0.20*	-0.06	0.23**			
Ear aspect	0.11	-0.01	-0.12	0.34***		
Grain yield	-0.21**	-0.16*	-0.06	-0.43***	-0.37***	

*, **, *** indicate significance at 0.05, 0.01, and 0.001 probability levels.

6.4 Discussion

6.4.1 Selection gain for weevil resistance

Results of the response of cycles C_0 , C_1 , and C_2 to artificial weevil infestations revealed significant differences among the three populations, with better performances exhibited in advanced populations. These results suggested that the source population (Longe5) positively responded to selection. The better performance of advanced populations suggested that each cycle of selection was accompanied by a gain in selection. Thus the more selections executed the better the advanced cycle is expected to perform; this was exhibited in the performance of cycles C_2 , C_1 , and C_0 as regards to percent kernel damage, whereby C_2 outperformed C_1 , which in turn was better than C_0 . However, it would be necessary to establish the limit towards the gain in selection. Selection gains for weevil resistance have been reported in a few maize populations (Dhliwayo and Pixley, 2003; Van Schoonhoven et al., 1975).

The significantly higher number of live weevils exhibited in grain obtained from Masaka than the grain from Namulonge and Serere could be attributed to genotype x environment interactions. The effects of genotype x environment interactions have been reported to affect grain susceptibility towards infestation by the maize weevil (García-Lara et al., 2009; Tipping et al., 1989; Van Schoonhoven et al., 1975). Van Schoonhoven et al. (1975) reported variations in maize weevil resistance, in maize populations, arising from environmental factors in USA.

6.4.2 Realized gain for grain yield, texture and ear aspect, and towards foliar disease resistance

The results of the performance of cycles C_1 and C_2 and the performance of the source population (cycle C_0), revealed significant improvement in grain yield, texture and ear aspect resulting from selection for weevil resistance. The results indicated that selection and recombination of weevil-resistant agronomically superior genotypes from cycle C_0 , created favorable responses in the new populations, as manifested in the realized gains in selection in cycles C_1 and C_2 , towards improved grain yield, texture, and ear aspect, in addition to increased resistance against GLS, TLB, and rust. Improvement in maize grain yield as a result of selection against biotic factors has been reported elsewhere. Badu-Apraku et al. (2009) reported grain yield gains of up to 58% cycle⁻¹ in white maize populations, and up to 90% cycle⁻¹ in yellow extra early populations, from recurrent selection results against *Striga*, conducted under *Striga* infested environments in west Africa.

6.4.3 Correlations between the study parameters

For the grain susceptibility parameters, positive significant correlations were observed between grain weight loss and F_1 weevil progeny emergence, grain weight loss and kernel damage, and between F_1 weevil progeny emergence and kernel damage. These correlations confirmed the fact that a large number of F_1 weevil progenies emerging from the grain caused huge kernel damage, leading to large quantity of grain lost through feeding (Mwololo et al., 2012; Temesgen and Waktole, 2013)

The significant negative correlations exhibited between grain yield and grain texture implied that the lower the texture scores (more grain flintiness) the higher the grain yield. These results suggested that genotypes with flint kernels were heavier than those with dent kernels. The negative and significant correlation between grain yield and ear aspect suggested that genotypes with good ear aspect (low scores) exhibited high grain yield. Indeed, high proportions of well-developed big ears ought to yield heavily, as opposed to poorly developed small ears with large ear aspect scores. On the other hand, the negative significant correlations between grain yield and GLS, and TLB diseases implied reductions in grain yield resulting from increased severity of grey leaf spot (GLS) and *Turcicum* leaf blight diseases; the two being foliar diseases, increase in their severity would imply an increase in foliar tissue necrosis and thus a reduction in the photosynthetic tissue leading to a decline in production of assimilates required for grain

filling. The negative but insignificant relationship observed between rust and grain yield suggested that rust disease was not significantly reducing grain yield during the evaluation period; however, this may not necessarily be the case always.

The positive correlations between ear aspect and TLB, and grain texture and TLB indicated that an increase in TLB disease pressure led to a decline in ear aspect and grain texture. These results implied that high TLB severity reduced the photosynthetic area of the leaves through increased leaf necrosis, thereby reducing the source of assimilates that would have improved the ear aspect and grain texture. These results are in agreement with Pataky et al. (1998) who reported reduced ear aspect and weight in plots heavily infested by TLB as opposed to plots with minimal TLB.

Absence of significant correlations between GLS and TLB, and GLS and rust suggested the independence of the three diseases hence they can be expressed independently. These results are in agreement with Vivek et al. (2010) who observed non-significant correlations between GLS, TLB, rust, head smuts, Ear rots, maize streak virus, and *Phaeosphaeria* leaf spot (PLS). The lack of association among the foliar diseases listed implies that their control can be effected through gene pyramiding.

6.5 Conclusion

Based on the significant reduction in F_1 weevil emergence, in addition to the three fold reduction in percent kernel damage and grain weight loss between C_2 and C_0 , it was evident that the two cycles of modified S_1 recurrent selection were effective in improving Longe5 for weevil resistance. The more than 29% increment in yield and more than 15% reduction in TLB, GLS, and rust diseases from C_0 to C_2 demonstrated the potential for improving these traits alongside selection for improvement of weevil resistance in Longe5.

The better performance of cycle C_2 than cycle C_1 , which was also better than cycle C_0 in most of the traits, suggested that advancement to more cycles of selection would lead to further improvement in the study traits; therefore, more selection cycles would be required in subsequent studies, in order to explore maximum selection gain. This further suggested the need to advance selections on the cycle C_2 seed generated from this study, for development of a new version of Longe5.

The superior performance manifested by cycle two (C_2), as regards to weevil resistance, grain yield, and resistance to TLB, GLS, and rust ought to be exploited hence necessitating its deployment for commercial production.

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Chapter Seven

Comparing the effectiveness of the “weevil warehouse” and “laboratory bioassay” as techniques for screening maize genotypes for weevil resistance

Abstract

Maize (*Zea mays* L.) grain resistance against the maize weevil (*Sitophilus zeamais* Motsch.) is the most sustainable control measure aimed at maintaining grain quality, while at the same time minimizing postharvest weight losses. Therefore, proper identification of weevil resistant donor parents would be a vital step in maize weevil resistance breeding programs. A simple, inexpensive, time saving and precise maize screening technique would be desired for effective discrimination of germplasm into different weevil response classes. The current study compared the effectiveness of the weevil warehouse (free-choice) screening technique with the laboratory bioassay (no-choice) technique towards discriminating maize genotypes into different susceptibility classes. The specific objectives of the study were to compare the effectiveness of the shelled grain and suspended ear options of the weevil warehouse technique and the laboratory bioassay technique in discriminating maize genotypes for maize weevil resistance. Secondary to determine the minimum period required for the protocol to be completed. Fourteen maize genotypes were simultaneously screened using the weevil warehouse and the laboratory bioassay techniques. The grain damage and grain weight loss parameters were measured. High levels of consistency were observed during grouping of genotypes into different response classes by the two methods indicating that they were equally effective. Therefore, the weevil warehouse technique is recommended as an effective maize screening method. The minimum evaluation period required to discriminate genotypes was two months from the onset of the experiment.

Key words: Host plant resistance, maize, screening for weevil resistance.

7.1 Introduction

Germplasm screening is a vital step in maize weevil resistance breeding programs. However, for effective identification of weevil resistant genotypes, a fast, cheap and precise maize screening method would be required. Various screening procedures have been used to discriminate maize germplasm into different susceptibility classes (Derera et al., 2010; Urrelo et al., 1990; Dobie, 1974; Widstrom et al., 1972). Widstrom et al. (1972) reported that F_1 weevil progeny emergence was a more consistent parameter for discriminating maize genotypes into different weevil susceptibility classes, as opposed to parental weevil mortality. Dobie (1974) developed one of the most popular screening methods that utilizes F_1 weevil progeny emergence and the median development period (MDP) to constitute the Dobie index of susceptibility (DIS). The DIS discriminates maize genotypes into resistant, moderately resistant, moderately susceptible, susceptible, and highly susceptible, based on the magnitude of the index. The smaller the index the more resistant against weevils the genotype is and vice versa. The DIS deploys laboratory based bioassay procedure that exploits the “no-choice” screening option. Generally, the Dobie (1974) method requires a long screening period and labour, in addition to the laboratory equipment requirements. Breeders require a rapid method for screening genotypes so that they can select and plant in the same year.

Various attempts have been made to reduce the time requirement of the DIS (Derera et al., 2010; Urrelo et al., 1990). Urrelo et al. (1990) modified Dobie’s (1974) technique by substituting F_1 progeny emergence with the number of egg plugs, and the MDP with days to first emergence. The new index developed by Urrelo et al. (1990) would be saving on the time required for the screening process, however, it requires more labour for counting the egg plugs especially at the initial stages (Gudrups et al., 2001). It also requires the use of chemicals and more skills in identifying the egg plugs through a staining technique and thus it is expensive. Derera et al. (2010) developed a rapid maize screening protocol by modifications on the Dobie (1974) method, through adjusting the oviposition period and the number of adult maize weevils required for screening maize genotypes, without sex determination which requires great skills and takes long time to complete.

Most of the maize screening methods reported are laboratory based protocols involving laboratory bioassays. In spite of the laboratory bioassay technique being popular, and hence a standard procedure, it requires high capital investment in terms of equipment, skilled personnel,

and also requires a long period of time from weevil-culture establishment to completion of the assessment. Furthermore, the laboratory bioassay system utilizes artificial screening conditions, which may not fully simulate the natural conditions under which the maize would be vulnerable to weevil attack. Consequently, variations in genotype response to weevil infestations may be manifested as a result of changes in the screening environmental conditions (Giga et al., 1999). Therefore, a simple, cheap and effective maize screening procedure that simulates farmers' storage conditions is required.

The weevil warehouse is a screening technique that would closely imitate farmer storage conditions. It exploits the free-choice screening option which portrays grain storage conditions for different maize varieties stored under farmer and/or trader situations and thus the results it generates would be more representative of farmer based results than the bioassay approach. Reports from previous studies indicate that the free-choice screening method of maize genotypes against weevils is effective as a preliminary screening procedure for identifying donor parents for weevil resistance breeding (Kang et al., 1995). Thus, the effectiveness of the free-choice screening method has not been fully explored in advanced evaluations of maize germplasm for weevil resistance. The current study explored the potential of the free-choice maize screening procedure, by comparing the effectiveness of the weevil warehouse to the standard "no-choice" screening procedure developed by Dobie (1974).

The objectives of the study were to: i) compare the effectiveness of the shelled grain and suspended ear options of the weevil warehouse and the laboratory bioassay technique in discriminating maize genotypes into different weevil susceptibility classes; ii) determine the minimum time required to discriminate maize genotypes into different susceptibility classes. The "free-choice" screening methods (options) in this study were exhibited in the weevil warehouse techniques, as unshelled ears suspended in the maize crib and shelled maize grain placed in paper bags and evaluated for weevil infestation and damage under crib conditions.

7.2 Materials and methods

7.2.1 Germplasm

The study materials were single cross hybrids from CIMMYT-Zimbabwe, inbred lines and open pollinated varieties from Uganda; the list of the 14 maize genotypes used in the study is

presented in Table 7.1. Genotypes M9 (Genotype # 10 [weevil/CML312]-B-13-2-1-BBB/[weevil/CML387]-B-9-1-1) and M10 (Genotype # 11 07WEEVIL) from CIMMYT-Zimbabwe were used as resistant checks, while genotypes M11 (Longe5) and M12 (orange popcorn variety) were used as susceptible checks.

7.2.2 Germplasm multiplication

To obtain enough ears for the study, the genotypes were first planted at the National Crops Resources Research Institute (NaCRRI), Namulonge (0°32'N, 32°34'E, 1200 m.a.s.l.) for multiplication purposes. The screening experiments were conducted for two seasons, in 2011B and 2012A. Ears used in 2011B screening were multiplied in the 2011 first rainy season (2011A), while the ones used in 2012A screening were multiplied in the 2011 second rainy season (2011B). To maintain the genetic composition of the genotypes, the genotypes were sib-mated and covered with tassel bags until harvesting.

7.2.3 Experimental setup and data collection

In 2011B season, one bioassay and one weevil warehouse screening experiments were executed; while in 2012A season, one bioassay and two weevil warehouse experiments were conducted. For all experiments the ears were harvested at dry maturity, and were de-husked according to their genotype numbers. After de-husking, the ears were sun dried until a moisture content of 13 – 15%; after which they were divided into two batches for the 2011B experiments. For the 2012A experiments the ears were divided into three batches. For the 2011B experiments, the first batch comprising of about 10 ears was shelled to obtain grain for the bioassay experiment, whereas the second batch comprising of about 20 uniform ears was prepared for the weevil warehouse experiment. For the 2012A experiments, the first batch of ears was prepared for the laboratory bioassay experiment. The second batch of ears was used for screening unshelled ears, while the third batch was shelled for screening as grain. The second and third batches were both screened under the weevil warehouse (free-choice) screening technique. All experimental materials were first subjected to cold treatment at -20°C for 14 days, to ensure that no live insects existed in any of the genotypes (ears) at the onset of the experiment.

Table 7.1: Genotypes used in the screening experiments

Code	Genotype number	Type of germplasm	Origin	Response to weevils
M1	Genotype # 1 CL106507	Inbred line	CIMMYT-Zimbabwe	Not known
M2	Genotype # 2 CL106508	Inbred line	CIMMYT-Zimbabwe	Not known
M3	Genotype # 3 CL106509	Inbred line	CIMMYT-Zimbabwe	Not known
M4	Genotype # 5 CL106511	Inbred line	CIMMYT-Zimbabwe	Not known
M5	Genotype # 6 CL106512	Inbred line	CIMMYT-Zimbabwe	Not known
M6	Genotype # 7 CL106513	Inbred line	CIMMYT-Zimbabwe	Not known
M7	Genotype # 8 CL106514	Inbred line	CIMMYT-Zimbabwe	Not known
M8	Genotype # 9 CL106515	Inbred line	CIMMYT-Zimbabwe	Not known
M9	Genotype # 10 [weevil/CML312] -B-13-2-1-BBB/[weevil/CML387]-B-9-1-1	Hybrid	CIMMYT-Zimbabwe	Resistant
M10	Genotype # 11 07WEEVIL	Inbred line	CIMMYT-Zimbabwe	Resistant
M11	Longe5	OPV	Uganda	Susceptible
M12	Popcorn	Landrace	Uganda	Susceptible
M13	WL-118-9	Inbred line	Uganda	Resistant
M14	WL-118-3	Inbred line	Uganda	Resistant

7.2.4 Laboratory bioassay technique

After cold treatment, grain for the no-choice screening technique was acclimatized for seven days under a weevil-free environment, after which 50 g were weighed into 250 cm³ glass jars with perforated lids fitted with <1 mm mesh for ventilation and blockage of weevil escape. Thirty two unsexed adult weevils of age 0 to 7 days (reared from the same laboratory) were used to infest the grain (Derera et al. 2010). The experiment was arranged in a randomized complete block design with six replications. The incubation conditions and period for the weevil-grain cultures were maintained as described in Chapter Three, section 3.2.5. The data collected included: the number of parental weevils alive and dead after 14 days, the total number of F₁ weevil progenies that emerged from each genotype, and the median development period (MDP), which was the period in days between the middle of oviposition to 50.0% emergence of the F₁ weevil progenies.

7.2.5 The weevil warehouse maize screening technique

The weevil warehouse technique involves screening of maize genotypes in a setup simulating farmer storage conditions, with minimal control over the storage conditions (temperature and relative humidity). This technique usually embraces free-choice screening methods, which for this study entailed unshelled maize ears suspended in nylon mesh bags and shelled grain put in paper bags according to Bergvinson (2006), modified by provision of adult maize weevils to enhance grain infestation.

7.2.5.1 Weevil rearing

Weevils for the free choice screening techniques were reared in the same maize crib where screening was carried out. Weevils used for the screening evaluations in the second season of 2011 (2011B) were reared between July and August of 2011, while the ones used in 2012A season were reared between January and February 2012. Weevil rearing was usually done about six weeks before the screening experiments commenced. The original parental weevils were sourced from infested maize grain in the nearby storage facilities. The infested maize grain obtained from the storage facilities, was sieved to separate weevils from the grain; afterwards about 500 weevils were introduced into 3000 cm³ plastic jars containing about 1.5 kg of well cleaned maize grain of the weevil susceptible variety Longe5. To obtain an adequate number of

weevils for the two experiments, 10 plastic jars were used. The plastic jars were covered with a muslin cloth to allow ventilation, and were fasted with a rubber band to stop weevils from escaping. The grain-weevil cultures were kept in the cribs under the prevailing temperatures⁴ that usually ranged from 16.2°C during the cold nights, to 32.3°C during the warm days; and the relative humidity range was between 55 and 89%. The plastic jars were monitored for freedom from diseases, whatever jars were found diseased (especially with molds) were discarded. An adequate number of weevils were raised in about 35 - 42 days.

7.2.5.2 Infestation of suspended ears

The second batch of ears was screened as intact ears (suspended ear option) using the weevil warehouse (free-choice) technique. Four uniform sized ears from each of the 14 test genotypes were put in mesh bags (onion bags), weighed to determine their original weights, and suspended on rafters of the maize crib (Figure 7.1). For purposes of experimental precision, the distance from one sample to another was maintained at 30 cm. Similarly, the distance from the crib floor to the suspended maize ears was uniformly 1 m. Overall, six replications were used per genotype, and were arranged in a randomized complete block design, thus a total of 84 mesh bags were used for the entire experiment. The experiment was divided into two sets, each set comprising of three replications. The first set was left intact for the four-month experimental period, after which they were weighed and scored for weevil damage. The second set was examined every month for taking record on the monthly weight loss, and grain damage until after the fourth month when the experiment was discontinued, due to time constraint. The second set was designed to determine the minimum period required to discriminate genotype susceptibility to weevil infestation. Infestation was effected by opening six plastic jars each containing 1400 – 1500 adult weevils. The weevils had been separated from infested grain by gentle sieving, prior to the experiment. In total, 8400 – 9000 adult weevils were used for infestation, which was on average 100 – 110 weevils per sample of the test genotypes. The plastic jars were arranged in the crib in such a way that all suspended ears stood equal chances of being infested at the same time and by the same number of weevils, when searching for new food (suspended ears). Infestations from other insects were minimized by fitting a gauze-wire mesh of pore sizes ≤ 1 mm at the sides of the maize crib, which was reinforced with a chicken

⁴ Temperature and relative humidity data were obtained from the Department of Meteorology, Ministry of Water and Environment, Uganda.

wire mesh to block rats from entering and destroying the experiments. Scoring for ear damage by the weevils was done using the scale of 1 to 10, according to Tefera et al. (2010): where 1 = 0 to \leq 10% damage, 2 = 11 to 20% damage, 3 = 21 to 30% damage, 4 = 31 to 40% damage, 5 = 41 to 50% damage, 6 = 51 to 60% damage, 7 = 61 to 70% damage, 8 = 71 to 80%, 9 = 81 to 90% damage, and 10 = 90 to 100% damage (Figure 7.2).



Figure 7.1: Weevil warehouse technique (suspended ear option), maize ears suspended in the maize crib.

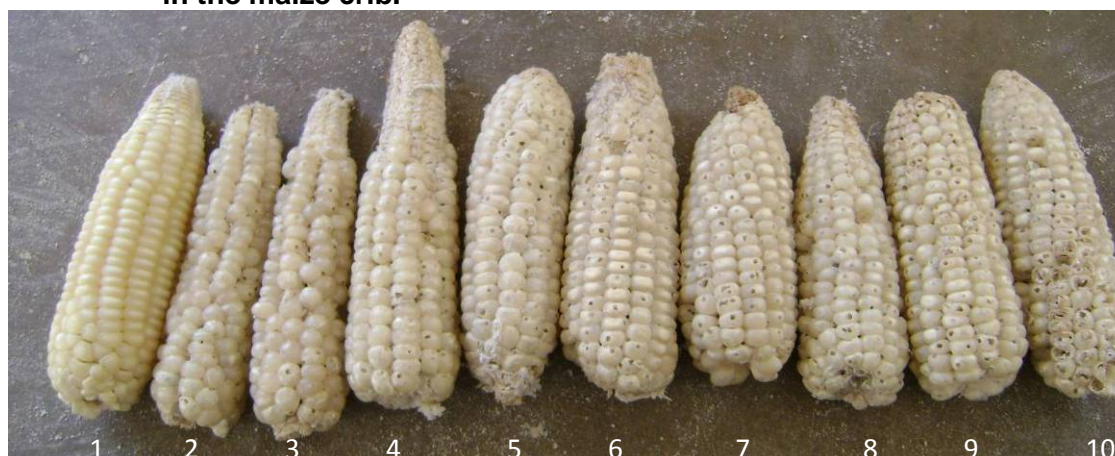


Figure 7.2: Representative scale of 1 to 10 used for scoring genotype response to weevil infestation.

7.2.5.3 Infestation of shelled grain

The third batch of ears was screened as shelled grain under the weevil warehouse (free-choice) screening method (Figure 7.3). One hundred grams of grain from each of the fourteen genotypes were weighed and separately put into paper bags of size 10 x 10 x 15 cm, length x width x height, respectively. Small holes that could not allow the maize grains to fall out of the paper bags were punched at the sides of the paper bags to enhance weevil genotype. Fourteen paper bags each containing one study genotype were randomly assigned into plastic buckets. The paper bags were put at the sides (walls) of the bucket, in order to maintain a uniform distance between them and the source of weevils that was placed in the centre of the bucket. This ensured that all study genotypes stood an equal chance of being infested at the same time and by the same number of weevils during the experiment. The source of weevils for infestation was a 250 cm³ glass jar containing 700 adult weevils. When the experiment was fully set, the glass jars were opened to allow weevils to move towards the test genotypes of their choice. Six buckets each containing 14 genotypes served as a complete replication. Thus, the experiment consisted of six replications, arranged in a randomized complete block design. The six replications were divided into two sets of three replications each. The first set was left intact until the end of the experiment, after 120 days. The second set was used for monthly data collection, to determine the minimum period in months, required to discriminate genotype susceptibility to weevil infestation. For both sets, data were recorded on grain weight, grain damage, weight of damaged and undamaged grains. Weight loss was determined as the difference between the original (100 g before infestation) and the new weight after infestation. Percent weight loss was then calculated according to Gwinner et al. (1996) as follows:

$$\text{Percent weight loss} = (W_u \times N_d) - (W_d \times N_u) \times 100 / W_u \times (N_d + N_u);$$

where W_u = weight of undamaged grain, N_d = number of damaged grains, W_d = weight of damaged grains, N_u = number of undamaged grains.



Figure 7. 3: Grain infestation with the maize weevil under shelled grain option of the weevil warehouse technique

7.2.6 Data analysis

The data obtained on the various parameters (yield loss, median development period, Dobie's index of susceptibility, percent kernel damage) were subjected to statistical analysis in SAS version 9.1, using general linear models (SAS-Institute, 2003). The differences between means were detected using least significant differences at a 5% probability level (LSD = 0.05). Genotypes were ranked according to their response to weevil infestation using SAS procedure Proc Rank.

Overall genotypic response to weevil infestation was derived from the following models:

Genotype response to weevil infestation: $Y_{ij} = \mu + R_i + E_j + e_{ij}$

where Y_{ij} = observed value of the trait; μ = overall mean of the trait; R_i = effect of the i^{th} replication ($i = 1, 2, 3, 4, 5, 6$); E_j = effect of the j^{th} genotype ($j = 1 \dots 14$); and e_{ij} = residual effect; while the monthly period response to weevil infestation was estimated from the following model:

Monthly response to weevil infestation: $Y_{ijk} = \mu + R_i + P_j + E_k + EP_{ik} + e_{ijk}$

where Y_{ijk} = observed value of the trait; μ = overall mean of the trait; R_i = effect of the i^{th} replication ($i = 1, 2, 3, 4, 5, 6$); P_j = effect of the j^{th} period (month) ($j = 1, 2, 3, 4$); E_k = effect of the k^{th} genotype ($k = 1 \dots 14$); EP_{ik} = effect of the interaction of the k^{th} genotype in the j^{th} period (month); e_{ijk} = residual effect.

Comparisons were based on the effectiveness of the three grain screening techniques towards ranking the study genotypes into the same response categories (resistance, moderate resistance, moderate susceptibility and susceptibility). The higher the level of consistence in ranking similar genotypes into the same response class, the closer the screening techniques would be in their efficiency towards genotype discrimination against weevil infestation. Therefore, the higher the possibility of one grain screening technique would be to effectively substitute the other one.

7.3 Results

7.3.1 Genotype response to infestation with the maize weevil

The mean squares for grain damage and grain weight loss exhibited in the 14 genotypes under laboratory bioassay, shelled grain and suspended ears techniques are presented in Table 7.2. The results indicated that genotypes were highly significant ($P < 0.001$) for the two grain susceptibility parameters assessed.

Table 7.2: Mean squares for grain damage and grain weight losses as exhibited in the 14 genotypes

Source	DF	Mean squares					
		Laboratory bioassay		Shelled grain		Suspended ears	
		GD (%)	GWL (%)	GD (%)	GWL (%)	GD (Score 1-10)	GWL (%)
Rep	5	7.48	19.73	32.24	5.45	8.55	5.79
Genotype	13	819.25***	261.23***	704.02***	550.52***	1883.94***	206.42***
Error	65	13.27	10.06	19.71	15.29	12.32	10.76
R²		0.93	0.84	0.88	0.88	0.97	0.80
CV (%)		6.55	13.27	7.11	12.24	6.87	17.55

*** = Significant at 0.001, GD = grain damage, GWL = grain weight loss.

7.3.2 Response of the 14 maize genotypes to weevil infestations as exhibited by different parameters.

The response to weevil infestation and the ranks of the 14 maize genotypes as exhibited by grain damage and weight loss encountered under laboratory bioassay and weevil warehouse conditions (shelled grain and suspended ear options) are shown in Table 7.3. Results of comparative assessment indicated significant ($P < 0.05$) differences among the 14 genotypes' response to weevil infestations under laboratory bioassay, shelled grain and suspended ear screening methods as manifested by grain damage and grain weight loss parameters.

For grain damage (GD), more damage was encountered under shelled grain than it was under laboratory bioassay and suspended ear techniques. Grain damage in shelled grain ranged from 49.3% in the resistant check M9 to 83.7% in genotype M7. The resistant check M9 was followed by genotypes M6, M13, M8, M14, M3, M1, M10, M4, M5, M11, M2, M12 and M7 in their order of increasing susceptibility. The response of genotypes M6, M8, M13 and M14 did not significantly ($P > 0.05$) differ from that of the resistant check M9; while the response to weevil attack by genotype M2 did not significantly differ from the susceptible check M12. For laboratory bioassay technique, genotype M13 was the least damaged (35.8%), while genotype M12 was the most damaged (70.7). Genotype M13 was followed by genotypes M8, M10, M3, M14, M6, M9, M11, M5, M2, M4, M7, M1 and M12 in their order of increasing percent grain damage. As regards to grain damage encountered under suspended ear technique, it ranged from 20.0% in genotype M13 to 76.67% in the susceptible check M11. Genotype M13 was followed by genotypes M3, M10, M8, M14, M4, M9, M1, M12, M6, M5, M7, M2, and M11, in their order of increasing susceptibility. Grain damage encountered by genotype M3 (25.0%) was not significantly ($P > 0.05$) different from that encountered by genotype M13. For the susceptibility class, genotypes M2 and M7 with grain damage of 74.8% and 72.5%, respectively, were not significantly ($P > 0.05$) different from the susceptible check M11. The remaining genotypes (M10, M8, M14, M4, M9, M1, M12, M6 and M5) encountered moderate grain damage.

For grain weight loss (GWL), on the other hand, the response of the 14 genotypes to weevil attack closely followed the same trend as that exhibited under grain damage (Table 7.3). Grain weight loss under laboratory bioassay technique ranged from 12.3% in genotype M8 to 32.3% in genotype M2. The weight loss encountered in genotypes M8 and M13 was 12.3 and 15.7%, respectively, which was not significantly ($P < 0.05$) different from the resistant check M9 that

encountered 13.7% weight loss. Grain weight loss encountered by genotypes M4, M5 and M14, and “resistant” check M10 was significantly higher than that of resistant check M9, but significantly lower than the susceptible checks M11 and M12. The remaining group of genotypes comprising of M1, M2, M7, and susceptible checks M11 and M12, encountered the highest percent grain weight loss of 30.1, 32.3, 29.2, 30.8, and 29.3, respectively.

Regarding grain weight loss encountered under shelled grain option of the weevil warehouse technique, it ranged from 17.3% in genotype M5 to 45.3% in genotype M1 (Table 7.3). Genotypes M4 and M5, and resistant check M14 encountered grain weight losses of 20.2, 17.3 and 19.5%, respectively, which were significantly lower than the rest of the genotypes. On the other hand, genotypes M1 and M7, and susceptible check M11 encountered weight losses of 45.3, 40.7 and 45.2% which were significantly higher than the rest of the genotypes. Grain weight losses encountered by genotypes M8, M12 and M13, and checks M9 and M10 were significantly higher than that encountered by genotypes M4, M5 and M14, but significantly lower than M1 and M7. For suspended ear option of the weevil warehouse technique, grain weight loss ranged from 7.9% in genotype M3, to 28.1% in susceptible check M12. Grain weight loss encountered by genotypes M3, M4 and M8 was 7.9, 10.7 and 11.7%, respectively, and this was significantly lower than 18.5, 18.5, 18.6, 18.3, and 18.2% which was encountered by genotypes M5, M6, M9, M10, and M13, respectively. The remaining genotypes M1, M2, M7, M11 and M12 encountered weight losses of 22.2, 26.2, 23.3, 24.0, and 28.1%, respectively which were significantly higher than the rest of the genotypes.

Table 7.3: Comparative assessment of the 14 maize genotypes under laboratory and weevil warehouse conditions

Genotype	Grain damage (%)						Grain weight loss (%)					
	Lab bioassay		Shelled grain		Suspended ears		Lab bioassay		Shelled grain		Suspended ears	
	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank	Mean	Rank
M1	70.17	13	60.83	7	54.67	8	30.08	12	45.03	14	22.17	10
M2	63.00	10	73.00	12	74.83	13	32.33	14	22.00	4	26.17	13
M3	45.17	4	59.33	6	25.00	2	27.17	9	39.17	11	8.00	1
M4	64.17	11	65.83	9	48.33	6	24.00	6	20.17	3	10.67	2
M5	57.67	9	67.83	10	63.00	11	24.50	7	17.33	1	18.50	7
M6	55.33	6	50.17	2	59.17	10	18.67	4	25.00	5	18.50	7
M7	69.83	12	83.67	14	72.50	12	29.17	10	40.67	12	23.33	11
M8	38.83	2	52.50	4	37.00	4	12.33	1	32.33	6	11.67	3
M9	56.83	7	49.33	1	49.17	7	13.67	2	35.83	9	18.60	9
M10	41.50	3	62.17	8	35.00	3	21.67	5	33.33	7	18.33	6
M11	57.67	8	70.67	11	76.67	14	30.83	13	45.17	13	24.00	12
M12	70.67	14	75.83	13	55.50	9	29.33	11	38.00	10	28.17	14
M13	35.83	1	50.33	3	20.00	1	15.67	3	33.50	8	18.20	5
M14	51.67	5	52.67	5	44.00	5	25.17	8	19.50	2	15.33	4
R²	0.93		0.88		0.97		0.84		0.88		0.80	
Trial mean	55.59		62.44		51.06		23.90		31.95		18.69	
LSD (0.05)	4.20		5.12		5.05		3.66		4.51		4.78	
CV (%)	6.55		7.11		6.87		13.27		12.24		17.55	

Ranks: 1 = best, 14 = worst, regarding the mean response of the 14 genotypes to weevil infestation, as assessed by grain damage and grain weight loss.

Generally, a reasonably high level of consistency was displayed when discriminating the 14 genotypes. For instance, genotype M13 was ranked among the resistant genotypes (ranks 1st to 3rd) by the three screening methods, while genotype M14 was ranked 5th by all the three screening methods under grain damage. Genotype M8 was ranked among the best six genotypes by the three screening methods under both grain damage and grain weight loss parameters; while genotype M10 was ranked 5th, 6th and 7th by laboratory bioassay, suspended ears and shelled grain, respectively. On the other hand, genotype M1 was consistently ranked in the susceptible category by the three screening methods i.e. 12th, 14th and 10th by laboratory bioassay, shelled grain and suspended ears, respectively under grain weight loss parameter; while for grain damage parameter, genotype M5 was ranked 9th, 10th and 11th by laboratory bioassay, shelled grain and suspended ears, respectively. Genotypes M2 and M7 were grouped in the susceptible category by the three screening methods (i.e. their ranks ranged from 10th to 14th under laboratory and weevil warehouse conditions) for both grain damage and grain weight loss parameters. Furthermore, genotypes M11 and M12 were both ranked among the susceptible genotypes by the three methods.

7.3.3 Correlation among genotype ranking by the three screening methods

Results of rank correlations by laboratory bioassay, shelled grain and suspended ear techniques, among the 14 genotypes based on their response to maize weevil attack are shown in Table 7.4. Significant positive correlations ($P < 0.05$ – $P < 0.01$) were exhibited among genotype ranking by laboratory bioassay, shelled grain and suspended ear techniques under grain damage and grain weight loss parameters. It was only ranking by shelled grain technique under grain weight loss parameter which exhibited insignificant ($P > 0.05$) positive correlations with the rest of the techniques.

Table 7.4: Correlation among ranks by laboratory bioassay, shelled grain and suspended ear techniques

	LGD	SGD	EGD	LWL	SWL	EWL
LGD						
SGD	0.67**					
EGD	0.67**	0.59*				
LWL	0.66*	0.75**	0.61*			
SWL	0.23	0.16	0.09	0.35		
EWL	0.65*	0.55*	0.76**	0.61*	0.37	

*, ** = 0.05 and 0.01 probability levels, respectively; LGD = grain damage under laboratory bioassay, SGD = grain damage under shelled grain, EGD = grain damage under suspended ears, LWL = grain weight loss under laboratory bioassay, SWL = grain weight loss in shelled grain, EWL = grain weight loss in suspended ears.

7.3.4 Monthly genotype response to weevil infestation

The mean squares for the monthly response of genotypes to weevil infestation, under weevil warehouse screening technique (shelled grain and suspended ears) are shown in Table 7.5. The mean squares indicated significant ($P < 0.05$ – $P < 0.001$) periods and genotypes for grain damage and grain weight loss, for both grains in paper bags and suspended ears. The interactions between the infestation period and genotypes were significant ($P < 0.001$) for grain weight loss under shelled grain and suspended ears. The interaction between infestation period and genotypes was significant ($P < 0.001$) for grain damage under suspended ears, but was not significant ($P > 0.05$) for grain damage under shelled grain.

Table 7.5: Mean squares for monthly grain damage and weight loss exhibited in shelled grain and suspended ears under the weevil warehouse screening technique during the four months' screening period

Source	DF	Mean square			
		Shelled grain		Suspended ears	
		GD (%)	GWL (%)	GD (Score 1-10)	GWL (%)
Rep	2	8.13	74.13	1.60	11.29
Period (P)	3	180.53***	6349.83***	177.48***	3974.85***
Genotype (E)	13	6.62*	338.29***	21.96***	140.12***
P*E	39	0.21	85.29***	1.86***	14.11***
Error	110	3.25	29.73	0.55	6.56
R²		0.65	0.89	0.94	0.95
CV (%)		46.76	35.79	17.31	12.19

*, *** = Significant at 0.05 and 0.001, GD = grain damage and GWL = grain weight loss.

Results of the monthly grain damage and weight loss under the weevil warehouse screening technique (shelled grain and suspended ears) are shown in Table 7.6. The results indicated significant differences among infestation periods for both grain damage and weight losses. Grain damage and weight losses were least in the first month and they significantly progressed in the subsequent months; however, due to time constraint assessments were stopped in the fourth month, in which the highest grain damage and weight loss were registered.

Table 7.6: Monthly grain damage and weight loss exhibited in the 14 genotypes

Period (Month)	Shelled grain		Suspended ears	
	GD (%)	GWL (%)	GD (Score 1-10)	GWL (%)
1	12.52	10.26	1.80	2.61
2	32.69	16.51	3.59	9.38
3	48.45	24.67	5.21	17.78
4	60.45	32.62	6.56	31.16
LSD (0.05)	7.79	1.11	0.32	2.36

GD = grain damage, GWL = grain weight loss.

7.3.5 Grain damage and weight loss exhibited among the 14 genotypes

Results of the monthly grain damage and weight loss encountered in the 14 genotypes during the four-month study period are presented in Figures 7.4 and 7.5, respectively. The results

revealed genotypic variations in response to weevil attack. Genotypes M2 and M4 encountered the least damage, followed by genotypes M10 (resistant check) and M14. Genotype M6 encountered the highest damage followed by genotype M11 (susceptible check) and M7 (Figure 7.4).

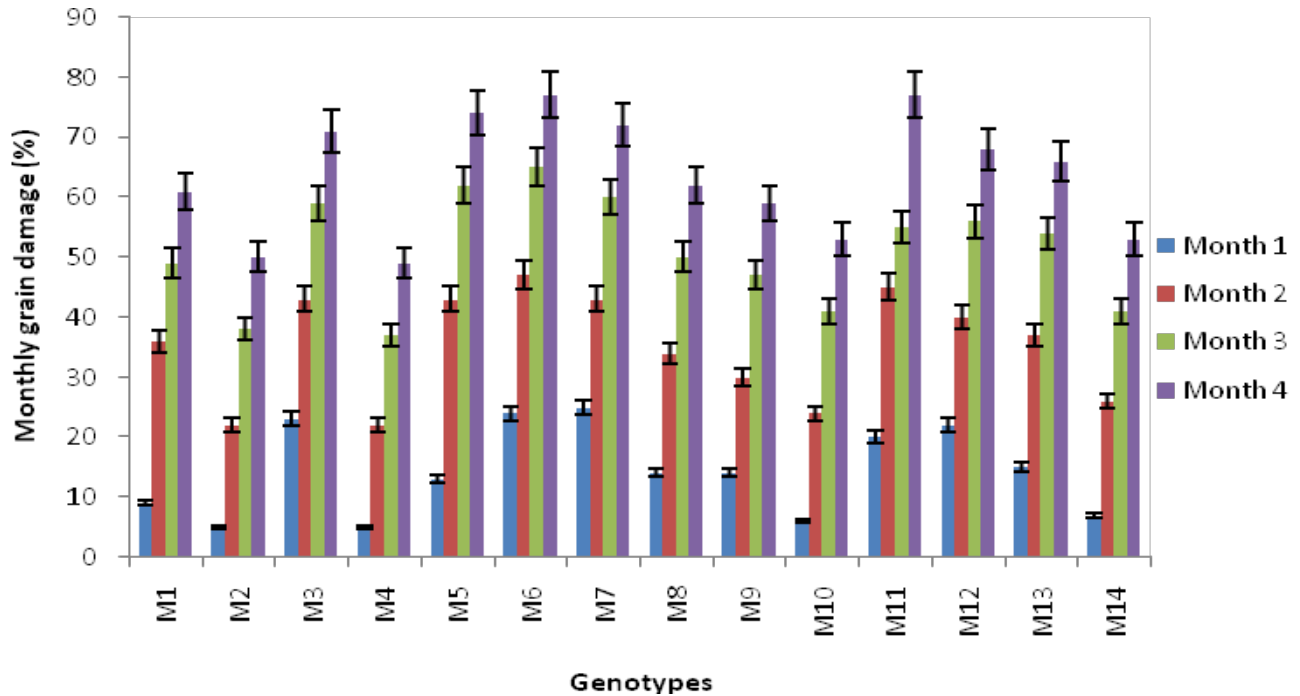


Figure 7. 4: Monthly grain damage encountered in the 14 genotypes during the four-month study period.

As regards to grain weight loss, genotype M9 (resistant check) encountered the least weight loss followed by genotypes M14, M4, M10 and M13 (Figure 7.5). Genotypes M11 and M12 (susceptible checks) encountered the highest weight loss. Generally, variations among genotype response to maize weevil attack were noted to decline as the study period progressed.

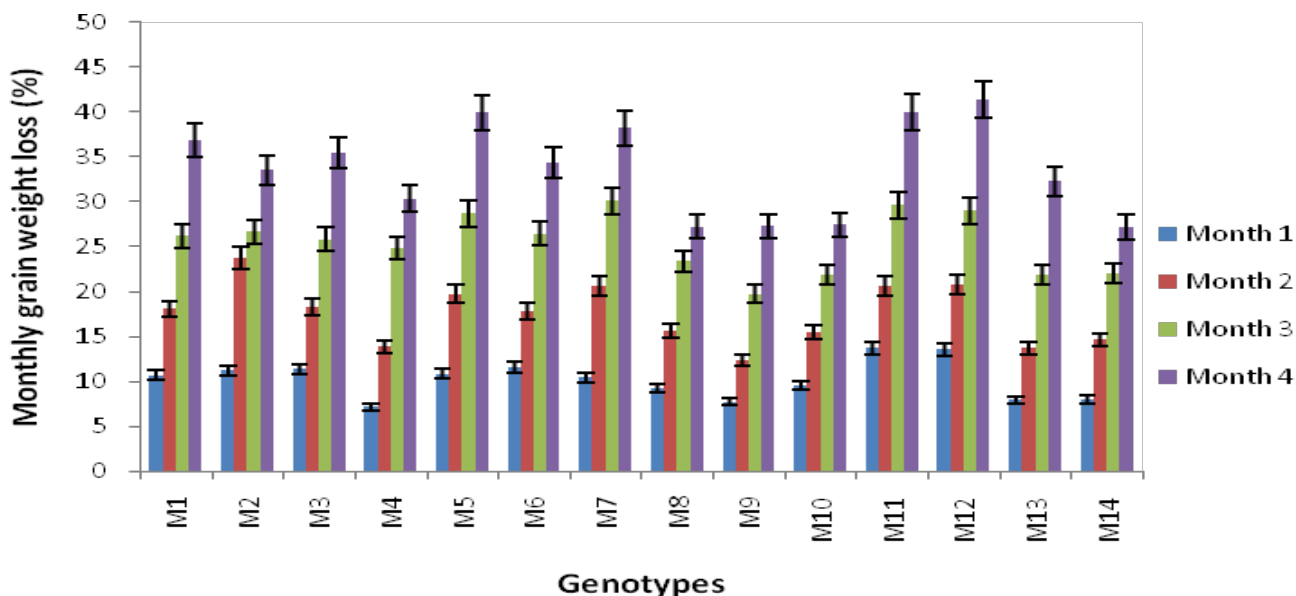


Figure 7. 5: Monthly grain weight loss encountered in the 14 genotypes during the four-month study period

7.4 Discussion

7.4.1 Genotype response to weevil infestation

The significant genotype mean squares for grain damage and grain weight loss indicated that the 14 genotypes responded differently towards weevil infestations under the three screening techniques. The results revealed the variations towards the response to weevil attack that existed among the 14 genotypes, which provided the basis for their discrimination.

Wide variations were observed among the 14 genotypes for the three maize screening techniques against weevil. As regards to grain damage, more damage was encountered under the “shelled grain” weevil warehouse screening technique than that encountered under the laboratory bioassay and suspended ear techniques. It ranged from 49.3% in resistant check M9 to 83.7% in genotype M7; whereas it ranged from 35.8 (M13) to 70.7% (M12) and from 20.0 (M1) to 76.7% (M11) for laboratory bioassay and suspended ear techniques, respectively. Generally, the higher grain damage levels encountered under shelled grain was probably due to the larger surface area exposed to weevils for attachment and subsequent boring, as compared

to the relatively smaller surface area exposed to weevils for attachment under unshelled (suspended) ears. These results are in agreement with Kossou et al. (1992) who reported reduced oviposition, increased median development period and subsequently less damage in unshelled maize ears than in shelled ears in Benin. The results are also consistent with the traditional practices by farmers, in Uganda, who store unshelled maize in cribs.

7.4.2 Genotype categorization

Based on grain damage and weight loss exhibited under the laboratory bioassay, shelled grain and suspended ear techniques, the 14 genotypes were grouped into three broad categories: resistant, moderately resistant and susceptible. The least, and the most damaged genotypes (which in most cases were one of the resistant and susceptible checks, respectively) were used as benchmarks for the groupings. Genotypes that were not significantly different from the least damaged genotype were categorized as resistant genotypes, whereas the ones that were not significantly different from the most damaged genotype were categorized as susceptible genotypes. For the genotypes that were significantly different from the two extremes were categorized as moderately resistant.

Grain damage in laboratory bioassays ranged from 35.8% in genotype M13 to 70.7% in genotype M12 (susceptible check). The damage sustained by genotype M8 (38.8%) was not significantly ($P>0.05$) different from the least damaged genotype M13 (35.8%); therefore, the two genotypes were categorized as resistant. On the other hand, genotypes M1 and M7 sustained high damages that were not significantly ($P>0.05$) different from the most damaged genotype i.e. susceptible check M12 and hence genotypes M1 and M7, in addition to check M12 were categorized as susceptible genotypes. The rest of the genotypes encountered grain damage that was significantly higher than the least damaged genotype (M13) and at the same time significantly lower than the most damaged genotype (M12) and hence were categorized as moderately resistant. Accordingly, the moderately resistant genotypes were M2, M3, M4, M5, M6, M9, M10, M11 and M14.

Regarding grain damage in shelled grain, genotypes M8, M9, M13 and M14 were categorized as resistant genotypes; genotypes M1, M3, M4, M5, M6, M10 and M11 were categorized as moderately resistant; while genotypes M2, M7 and M12 were categorized as susceptible. For grain damage under suspended ears, genotypes M3 and M13 were grouped in the resistant

class, genotypes M1, M4, M5, M6, M8, M9, M10, M12 and M14 were grouped in the moderately resistant class, while genotypes M2, M7 and M11 were grouped in the susceptible class. Based on this grouping criterion, a number of genotypes were observed to be consistently grouped in the same response category by the three screening techniques. For example, genotypes M3, M8 and M13 were consistently grouped in the resistant category by at least two of the three screening techniques. Similarly, genotypes M4 and M5 were consistently grouped in the moderately resistant category (except for grain weight loss under shelled grain), whereas genotype M7 was grouped in the susceptibility category by the three screening techniques. These results are in agreement with Giga et al. (1999) who reported comparable results between laboratory and on-farm maize evaluation techniques against weevil attack in Zimbabwe.

Regarding grain weight loss (%) the response trend exhibited was almost similar to that manifested under grain damage. Under laboratory bioassay technique, genotypes M4, M6, M8 and M9 were categorized as resistant, genotypes M3, M5, M10, M13 and M14 were categorized as moderately resistant, whereas genotypes M1, M2, M7, M11 and M12 were categorized as susceptible. For shelled grain, genotypes M4, M5 and M14 were categorized as resistant; genotypes M2, M3, M6, M8, M9, M10, M12 and M13 were categorized as moderately resistant, whereas genotypes M1, M7 and M11 were categorized as susceptible. For suspended ears, genotypes M3, M4 and M8 were categorized as resistant, genotypes M5, M6, M9, M10, M13 and M14 were categorized as moderately resistant, while genotypes M1, M2, M7, M11 and M12 were categorized as susceptible. From the response grouping based on grain weight loss parameter, it was also observed that some of the genotypes were consistently grouped in the same categories under the three screening techniques. For instance, genotype M4 was consistently grouped in the resistant category, genotypes M10 and M13 were consistently grouped in the moderately resistant category, whilst genotypes M1, M7 and M11 were consistently grouped in the susceptible category.

Reasonable levels of consistency were observed on grouping the 14 genotypes according to their response to weevil attack based on grain damage and grain weight loss, as assessed by laboratory bioassay and the weevil warehouse techniques (shelled grain and suspended ears). In all the three techniques, genotypes M8, M13 and M14 were ranked among the best six genotypes. Genotype M13 was ranked first by both laboratory bioassay technique and

suspended ear option, but ranked third by shelled grain option under grain damage. In a similar trend, genotype M8 was ranked fourth by both weevil warehouse techniques, and ranked second by the laboratory bioassay technique. Genotype M14 was ranked fifth by all the three techniques, thereby portraying the high level of consistency manifested by the three screening techniques.

On the other hand, genotypes M7 and M2, together with the susceptible checks M11 and M12 were consistently ranked among the worst six performing genotypes for grain damage encountered under the three screening techniques. In this regard, genotype M7 was ranked as the fourth last genotype for the laboratory bioassay technique and ranked the last by shelled grain, whereas it was ranked third last under suspended ears. All these ranks portray a reasonable level of consistency in genotype discrimination. These results are in agreement with Kang et al. (1995) who observed reasonable levels of consistency exhibited in experimental hybrids evaluated for response to weevil attack using the free-choice (shelled grain) screening technique.

7.4.3 Rank correlations

The significant positive correlations among genotype ranking by laboratory bioassay, shelled grain (only under grain damage) and suspended ear techniques emphasized the consistency exhibited during genotype categorization into different weevil resistance or susceptibility classes. The insignificant correlation between shelled grain under grain weight loss parameter and the rest of the techniques suggested that this technique was not appropriate for discriminating the 14 genotypes under the current study conditions.

7.4.4 Monthly response to weevil infestation

The mean squares of the monthly response of genotypes to weevil infestation, under weevil warehouse screening techniques indicated significant periods and genotypes for grain damage and grain weight loss, under both shelled grain and suspended ears (Table 7.4). This implied that the 14 genotypes exhibited significant differences in their response to grain damage resulting from weevil attack. The interactions between the infestation period and genotypes were significant ($P < 0.001$) for grain weight loss both under shelled grain and suspended ears (Table 7.4). The significant interaction between the infestation (incubation) period and genotypes implied that the 14 genotypes exhibited genotype-dependent variations in the rate of

grain damage and associated weight loss during the storage period. Genotype-dependent variations in response to weevil attack provided the basis for discriminating the 14 genotypes. These results are consistent with results reported by Giga et al. (1999).

Results of the monthly grain damage and/or weight loss indicated that the longer the grain was subjected to weevil infestations, the more grain damage was encountered and consequently the more weight of the grain was lost, however, the monthly responses (rate of grain damage and weight loss) were genotype dependent. The increased grain damage and subsequent weight losses were explained by the exponential increase in weevil population density resulting from multi-generation reproduction and continuous feeding on the same quantity of grain. Due to time constraint, the experiment was prematurely discontinued, therefore, the trend was not observed beyond four months; however, the rate of grain damage and weight loss was expected to decline as the evaluation period progressed, until a point it would level-off, when the food reserves in the grains are depleted. Nevertheless, grain damage and weight loss results portrayed a decline in genotypic variations in response to the maize weevil attack as the evaluation period progressed from the first to the fourth month. These results are consistent with those reported by Giga et al. (1999), who observed the narrowing of the gap between (decline in the variations) weevil susceptible and resistant genotypes as the incubation (storage) period increased.

Results from the current study indicated that a minimum of one month's storage was required to begin differentiating genotypes according to resistance or susceptibility. Genotype discrimination into different response classes would continue up to a point when susceptible genotypes cannot easily be distinguished from resistant ones. Giga et al. (1999) reported this period to be seven months of storage. To save on the screening time and associated screening costs including labour, discrimination of genotypes at early storage/incubation periods would be desirable. However, based on the screening protocols developed by Dobie (1974) and Derera et al. (2010), assessments of genotype response to weevil infestations were done using mainly the F_1 weevil progenies, which are expected to emerge from the grain between 28 and 60 days after oviposition under favourable conditions (Tefera et al., 2010). Therefore, a minimum period of two months of evaluation would be required for effective discrimination of genotypes, whereby at least the first F_1 weevil progenies would be involved in pest activities. However, the evaluation period could be extended up to six months (although more costs would be incurred)

beyond which the effectiveness in genotype discrimination tends to decline (Giga et al., 1999). Furthermore, a possibility of cross-infestation of weevils from the more susceptible genotypes (in which the food reserves are expected to be depleted faster) to the less susceptible genotypes may not be ruled out as the evaluation period progresses.

Based on the results, the weevil warehouse technique is observed as a simple and time saving maize screening technique that would effectively be used to discriminate maize genotypes based on their response to weevil attack. However, due to the high variations manifested within the same genotypes, more replications may be required and hence this technique would require much more quantities of the test maize grain and/or ears. Nevertheless, the weevil warehouse technique would be an appropriate screening technique for evaluating large numbers of maize genotypes within a short period of less than three months required for the laboratory bioassay technique.

7.5 Conclusion

The high levels of consistency displayed by the grain damage and grain weight loss parameters under the laboratory bioassay, shelled grain and suspended ear techniques suggested that the two parameters can effectively be used to discriminate maize genotypes under the three maize screening methods. This implies that either the shelled grain or the suspended ear option of the weevil warehouse technique can effectively be used to group maize genotypes into different susceptibility classes based on their response to weevil attack.

The minimum period required for effective discrimination of genotypes was two months during which F_1 weevil progenies are expected to have emerged and get involved in further pest activities against the test maize genotypes.

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Chapter eight

General overview

8.1 Introduction

This chapter summarizes the findings of the entire study, in addition to providing recommendations for different stakeholders. The overall objective of this study was contributing towards the reduction in postharvest yield losses associated with the maize weevil, through development of high yielding maize varieties resistant to the maize weevil and other biotic constraints. Therefore, most of the emphasis was put on efforts geared at enhancing maize productivity while at the same time ensuring minimal postharvest yield losses both at farmer and research levels. The key findings are presented based on the study objectives, while the implications and the way forward are generalized.

8.2 Key findings

8.2.1 Farmers' perceptions about weevil (*Sitophilus zeamais* Motschulsky) resistant maize cultivars

- The most important maize traits were yield, field pest and disease resistance, good storability/resistance to the maize weevil, drought and nitrogen stress tolerance;
- Over 95.0% of farmers knew the maize weevil and a number of them were controlling it through proper drying and addition of wood ash, red pepper, or botanicals such as *Cupressus sempervirens* to the grain; some farmers were applying chemicals, while others were selling grain early before weevils multiply to cause significant damage;
- Storage was reported as one of the major challenges in maize post-production. However, over 69.0%, 90.0%, and <20.0% of farmers in Kasese, Kapchorwa and Nakaseke districts, respectively, were using locally constructed structures as maize cribs for grain storage. Poor storage was partly the reason why farmers were selling their maize early.
- About 50.0% of the farmers were selling more than 50.0% of their maize within three months after harvesting. Some farmers were doing so in order to get cash for family obligations, while others were evading postharvest grain losses arising from weevil attack;

- Farmers estimated grain weight losses associated with the maize weevil after four months' storage period to be exceeding 20.0%;
- High grain infestation levels above 95.0, 85.0 and 55.0%, were observed in the maize grain samples from Kasese, Nakaseke and Kapchorwa districts, respectively;
- Only 25.0% of the farmers had easy access and hence were able to buy maize seed from reliable sources (agro-input shops), 47.0% of the respondents were buying seed from any sources, 18.0% were recycling seed, while 10.0% were usually depending on free seed from government, non government organisations and fellow farmers;
- The “older” Longe varieties mainly Longe1, Longe4, Longe5 and Longe6H were more popular in Kasese and Nakaseke districts than the “newer” varieties such as Longe9H, Longe10H and Longe11H. On the other hand, in Kapchorwa district there were no highland maize cultivars developed from Uganda save for H614D that was being imported from Kenya;
- The mean maize yields ranged between 1.00 and 2.00 t ha⁻¹ for about 50% of the farmers.

8.2.2 Genotypic variation for maize weevil resistance in eastern and southern Africa maize germplasm lines

- The proportion of resistant, moderately resistant, moderately susceptible, susceptible, and highly susceptible genotypes was 4.4, 10.6, 18.9, 36.1 and 30%, respectively;
- Inbred lines MV13, MV21, MV23, MV31, MV63, MV75, MV105, MV142, MV154, MV157, MV163, MV170, and MV175 were consistently ranked by the grain susceptibility parameters as the 13 most weevil resistant lines;
- Inbred lines MV13, MV21, MV31, MV63, MV75, MV142, MV154, MV163 and MV170 combined weevil resistance, resistance to diseases and yield;
- Inbred lines MV44 and MV102 were not weevil resistant but exhibited outstanding yield and disease resistance;
- Large heritability values, above 89.0%, were exhibited for weevil resistance in the four grain susceptibility parameters (F₁ weevil progeny emergency, grain damage, median development period and Dobie index of susceptibility);

- Moderately high heritability values were exhibited for yield, while low heritability values were exhibited for foliar diseases that naturally manifested during trial evaluations;
- Very low associations were manifested between DIS and yield, and foliar disease resistance.

8.2.3 Diallel analysis of grain yield and weevil resistance in eastern and southern Africa maize germplasm lines

- Additive gene action, non-additive gene action and maternal effects were all responsible for conditioning weevil resistance in F_1 hybrid seed, F_2 full-sib and F_2 half-sib grain generation;
- Maternal effects were “generally” the most important genetic effects conditioning weevil resistance in F_1 hybrid seed, generally, additive gene effects were the most important effects regulating weevil resistance in F_2 full-sib grain generation; whereas in F_2 -half-sib grain generation non-additive effects were the most important genetic effects responsible for weevil resistance. Hence weevil resistant maize cultivars can be developed through selection and hybridization. However, in order to minimize damage among parental lines, the seed parents ought to be weevil resistant;
- Hybrids MV75 x MV154, MV154 x MV142, MV142 x MV170, MV154 x MV31 and MV170 x MV13 were consistently ranked among the top 20 weevil resistant hybrids based on the F_1 weevil emergence from the three seed/grain generations, while hybrids MV170 x MV13 and MV75 x MV154 were ranked among the top 20 weevil resistant as well as among the top 20 stable high yielding materials;
- Parents MV170 and MV142 were significantly contributing towards a reduction in weevil emergence in F_1 hybrid seed, F_2 full-sib and F_2 half-sib grain and hence they were good general combiners;
- High levels of heterosis were manifested in hybrids generated by parental lines MV170 and MV142;
- Hybrids MV75 x MV142, MV142 x MV44, and MV31 x MV102 exhibited negative significant SCA effects towards weevil resistance in more than one seed/grain generation;

- Large proportions of SCA sum of squares were exhibited for grain yield in the experimental hybrids;
- High levels of heterosis for grain yield were manifested between crosses MV170 and MV75, MV142 and MV75, MV170 and MV102, MV170 and MV44, and MV170 and MV31;
- Hybrids MV154 x MV75, MV31 x MV170, MV75 x MV142, x MV31 x MV142, MV44 x MV21, MV44 x MV154, MV102 x MV13, MV31 x MV13, and MV44 x MV170 exhibited outstanding performance comparable to the local checks;
- Parental line MV44 from CIMMYT-Kenya exhibited positive and significant general combining ability (GCA) effects and generated a number of hybrids with outstanding performance.

8.2.4 Response of maize population “Longe5” to two cycles of modified S₁ recurrent selection for resistance to maize weevil.

- A three-fold reduction in percent kernel damage and grain weight loss was registered between cycles C₂ and C₀;
- Yield increment above 18% and above 15% reduction in *Turcicum* leaf blight (TLB), grey leaf spot (GLS), and rust diseases were registered between cycles C₂ and C₀;
- Increment in weevil resistance after the second selection cycle did not compromise grain yield in Longe5 population.

8.2.5 Comparing the effectiveness of the “weevil warehouse” and “laboratory bioassay” as techniques for screening maize genotypes for weevil resistance

- High levels of consistency were displayed by grain damage and grain weight loss parameters under the laboratory bioassay technique and the weevil warehouse technique;
- Both shelled grain and suspended ear options of the weevil warehouse technique can effectively be used to group maize genotypes into different susceptibility classes based on their response to weevil attack;
- The minimum period required for effective discrimination of genotypes was two months,

using grain damage parameter, for shelled grain technique under the weevil warehouse technique;

- The weevil warehouse technique is a relatively simple and time saving maize screening technique that can effectively be used to discriminate maize genotypes based on their response to weevil attack.

8.3 Conclusion

All in all, the maize weevil is noted to be an important storage pest constraining maize production in Uganda. The major weevil control measures include proper postharvest handling procedures and use of indigenous technical knowledge. Results also revealed that host plant resistance could significantly reduce grain damage. It was further revealed that grain resistance against the maize weevil could be enhanced through hybridization and recurrent selection. Ultimately, the study objectives were achieved as described below:

- Results from the current study revealed that farmers are aware of the maize weevil, associated damages to the maize grain, and the existence of weevil resistance in different maize cultivars. Thus the acceptance of the hypothesis that, “farmers are aware of the damages caused by the maize weevil to the maize grain during storage and believe that grain damage can be minimized through cultivation of weevil resistant maize varieties”;
- Genotypic variations for maize weevil resistance were observed among the maize germplasm lines obtained from eastern and southern Africa. This is in agreement with the hypothesis that, “maize germplasm lines from eastern and southern Africa exhibit genotypic variations in weevil resistance, therefore effective sources of resistance can be found and used for breeding new weevil resistant varieties”;
- Results of gene action conditioning maize weevil resistance in different seed/grain generations indicated that additive gene action, non-additive gene action and maternal effects were all responsible for conditioning maize weevil resistance in F_1 hybrid seed, F_2 full-sib and F_2 half-sib grains. This was partly in agreement with the hypothesis that, “weevil resistance in maize germplasm from eastern and southern Africa is controlled by genes with additive gene effects hence it can be improved through selection; and there is good specific combining ability for both yield and weevil resistance in the inbred line populations that would be exploited in designing hybrids and synthetic populations”;

- Two cycles of modified S₁ recurrent selection significantly improved Longe5 towards weevil resistance and agronomic superiority; thus accepting the hypothesis that, “the tropical maize population Longe5 can be improved for weevil resistance and agronomic superiority through modified S₁ recurrent selection;
- Finally, the results revealed that the “weevil warehouse technique” can effectively discriminate maize genotypes into different response classes towards weevil infestations, in comparison with the “laboratory bioassay technique”. Therefore, the “weevil warehouse technique” being faster and easier to execute, it can effectively substitute the “laboratory bioassay technique”. This is in agreement with the hypothesis that, “there are no differences between the effectiveness of the weevil warehouse technique and the laboratory bioassay technique in screening maize germplasm for weevil resistance; and each technique can effectively discriminate maize germplasm into different response classes without losing experimental precision”.

8.4 Recommendations

- The results indicated that: more training and sensitization would be required to enhance stakeholder capacity to control the maize weevil, especially through proper postharvest grain handling (to ensure sanitation during drying and storage). This will maintain high grain quality for both local and regional markets;
- The use of indigenous technical knowledge (ITK) in the control of the maize weevil, the efficacy of the local materials/substances such as wood ash, red pepper and *Cupressus sempervirens* ought to be established and validated;
- Since superior grain quality is the ultimate attribute desired by the consumers, efforts aimed at maintaining high grain quality are paramount. Therefore, it would be necessary to first screen newly released maize varieties, in order to establish their response to weevil infestations so as to develop appropriate management packages up to grain storage level;
- The parental lines identified to be good combiners for grain yield and weevil resistance are appropriate parents for development of high yielding maize weevil resistant hybrids and therefore would be required for advancement;

- The selection gain towards weevil resistance, yield enhancement and associated reduction in foliar disease expression registered in cycles C₁ and C₂ could be exploited by availing the new Longe5 maize populations (preferably cycle C₂) for commercial production and/or subject them to advanced cycles of selection with the purpose of generating a more superior population.