HOST-PLANT INTERACTIONS AND RESISTANCE MECHANISMS TO BANANA WEEVIL *COSMOPOLITES SORDIDUS* (Germar) IN UGANDAN *MUSA* GERMPLASM

by

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CHAPTER I

INTRODUCTION

Banana weevil (*Cosmopolites sordidus* Germar), found in all banana and plantain growing regions of the world. It represents the most serious insect pest to the crop in Africa, Asia and the Caribbean where production is mainly for subsistence. Damage is caused by the larvae, which tunnel into the underground stem as they develop. This tunnelling interferes with water and nutrient uptake, weakens the stem and acts as entry for secondary factors like bacteria and fungi which then lead to premature decay of the tissues. A plantation affected by high incidence of banana weevil will have considerable toppling and snapping of plants, poor plant development, and miserable bunch weights.

Banana is a staple food to more than 7 million people, constituting a major source of carbohydrate in their diet. Uganda is the second largest producer and consumer of banana in the world after India (Lescot, 1998). The annual production of Uganda alone is 9.7 million tonnes (Lescot, 1998) and the estimated per capita consumption is 150 kg per annum (Karamura and Karamura, 1995). The bananas are harvested green, steamed and mashed to make a dish called 'matooke', which is eaten with any vegetable sauce or meat stew. Bananas are also an important source of income to many farmers who produce for a growing urban market. Local wine and gin (called 'waragi') are produced from bananas and these products serve as a source of income to farmers in more remote areas, since 'waragi' keeps longer and can be transported on poorer rural roads to the cities. Other uses of banana include medicine, shelter material, livestock-feed, handicrafts and soil conservation material.

The production of banana in Uganda has steadily declined from about 12 million tonnes in the 1960's to the current 9.7 million tonnes. From results of two major nation-wide surveys, banana weevil was reported to be the single most important production constraint (Gold *et al.*, 1993). It has also been blamed as one of the major causes of geographic shifts of banana production, from traditional growing areas to new non-traditional areas (Gold *et al.*, 1999b). Other constraints like nematode root pests, diseases like Black Sigatoka and Fusariam wilt, declining soil fertility, land pressure, changing climatic conditions and socio-economic problems like labour, have also contributed to the decline in banana production (Gold *et al.*,

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CHAPTER II

LITERATURE REVIEW

2.1 Introduction

The aim of this chapter is to review various aspects of the banana host plant and the banana weevil (*Cosmopolites sordidus*) so as to put the reader in perspective *vis-à-vis* the relationships between these two organisms. Most importantly however, the chapter reviews recent literature surrounding host plant resistance, response of *Musa* germplasm and resistance mechanisms to banana weevil. The prospects for improving banana and plantain through conventional crossing and genetic engineering are also discussed and finally, the implications of host plant resistance as an integrated pest management component are highlighted.

2.2 Banana and plantain

Throughout this chapter the term banana is used to refer to dessert, cooking bananas and plantains. Plantains are essentially different from bananas because their fruit is too starchy to eat even when ripe and must be cooked. The term cooking banana being reserved for plantain can be confusing in some literature because in East Africa the type of bananas that are cooked are not plantains. The Food and Agricultural Organisation (FAO), production yearbooks erroneously refer to East African highland cooking bananas as plantains (FAO, 1993; Lescot, 1998).

2.3 Structure and morphology of *Musa*

Bananas are generally large herbaceous tree-like plants, semi perennial and monocarpic (*i.e.* each shoot dies after fruiting once). The above ground part consists of a pseudostem (false stem) made up of leaf sheaths tightly clasping each other. These sheaths are more swollen at the bottom making the lower part of the pseudostem larger than the upper part (Figure 2.1b). A leaf consists of a sheath, a petiole and the leaf blade. The leaves arise from the true

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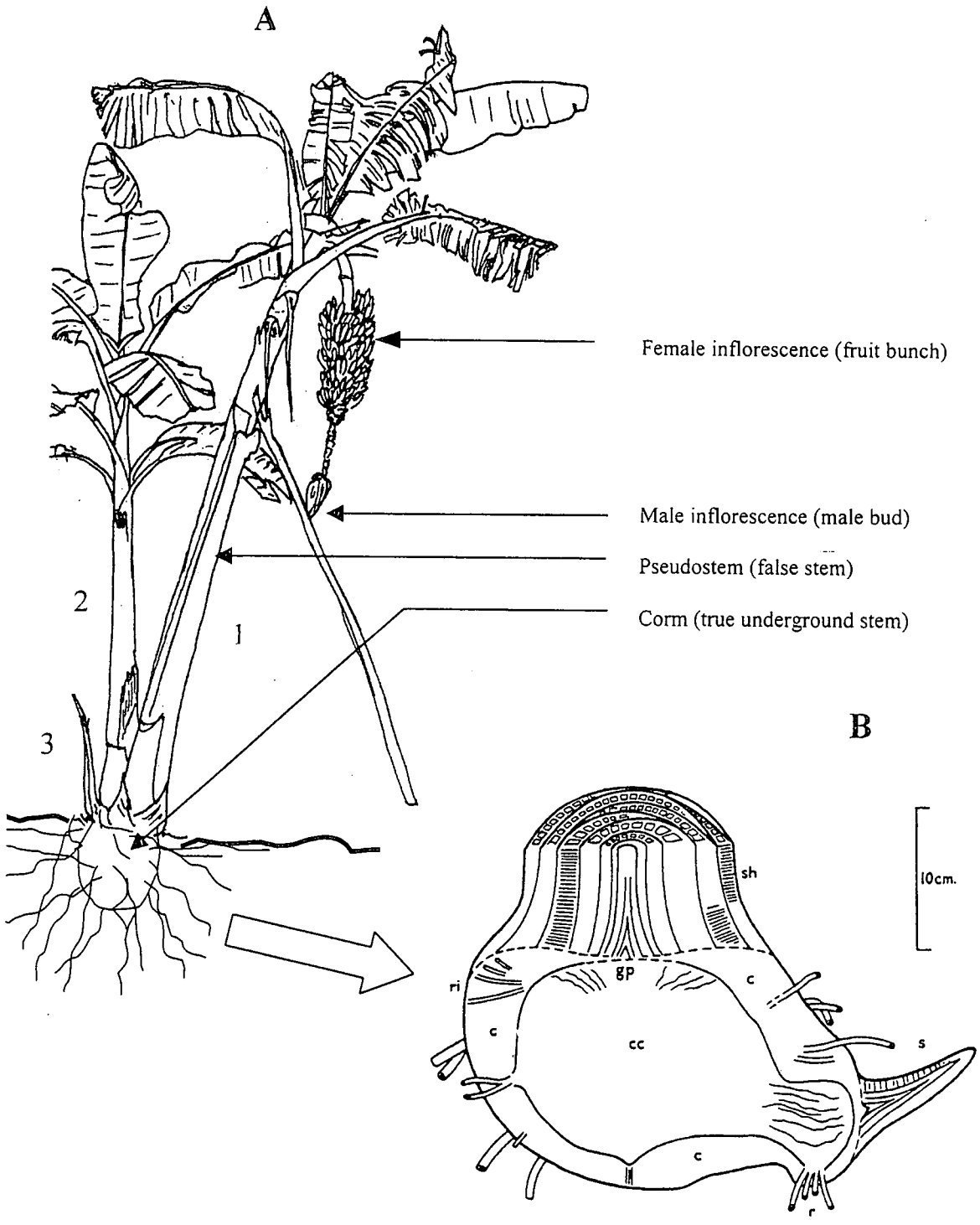
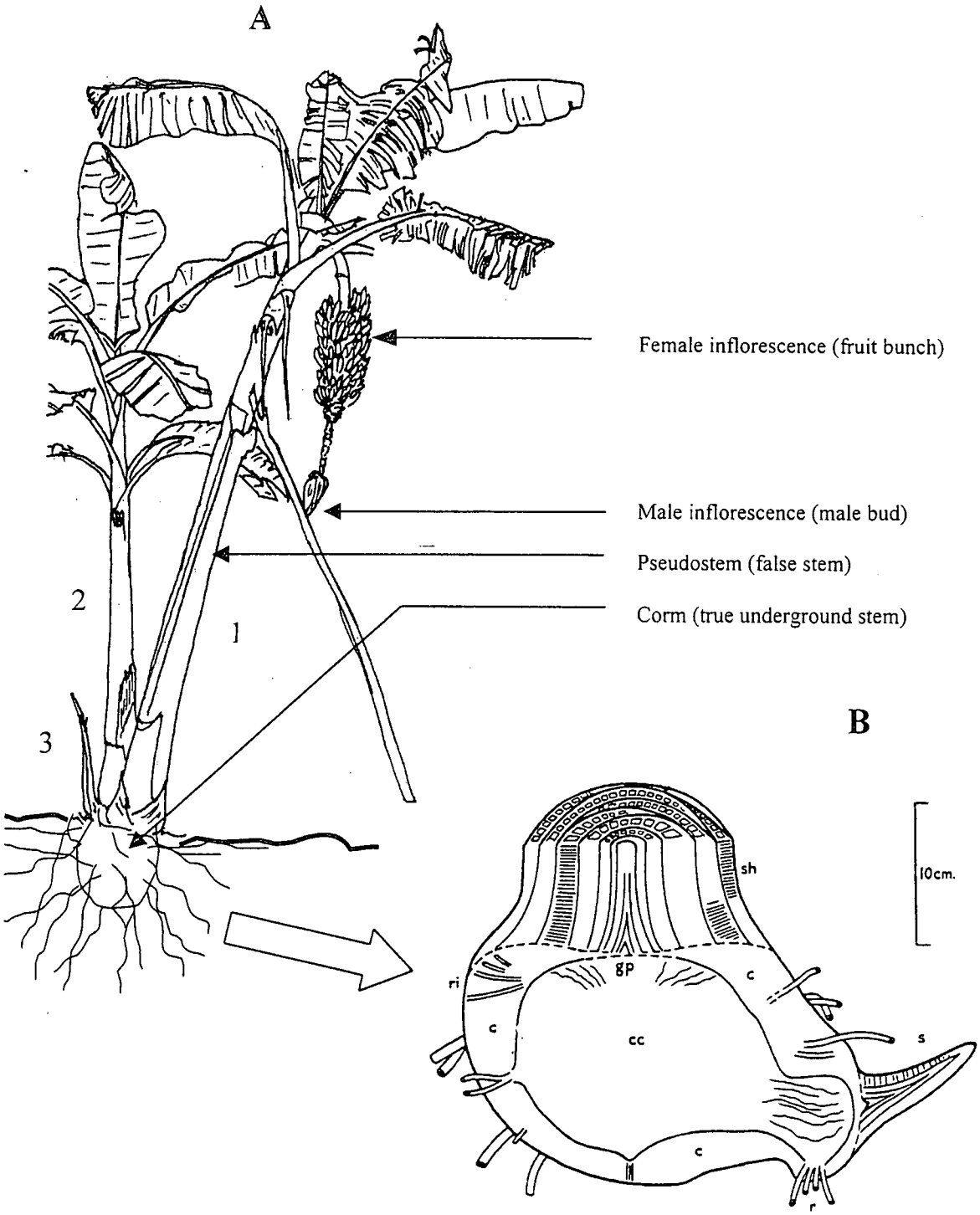


Figure 2.1 **A:** Structure of a typical East African highland banana plant (mat). 1-mother plant (flowered) 2-daughter plant (pre-flowered) and 3-sucker. **B:** Longitudinal section of the corm (underground true stem) (Modified from Simmonds, 1966), sh-leaf sheaths, s-sucker, gp-growing point (meristem), c-cortex, cc-central cylinder, r-roots.



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A unique group of bananas adapted to the highlands is the most important staple crop in the East African Great Lakes region. This region includes all the areas surrounding Lake Victoria, (East, Central and South Western Uganda, Northern Tanzania, and Western Kenya), Eastern Democratic Republic of Congo (DRC) (former Zaire), Rwanda and Burundi. This group of AAA genomic bananas is referred to as East African Highland Bananas (AAA-East Africa) and is divided into two types based on end use, namely cooking and brewing types. Uganda has the largest diversity of highland banana germplasm world-wide (Kyobe, 1981), with more than 200 different cultivars recorded from one survey (Gold *et al.,* 1998). Recently, using morphological taxonomic methods, the number of core cultivars has been reduced to 80 (Karamura, 1998). This diversity developed during the many centuries of native banana cultivation in Uganda, through *in situ* somatic mutations and selection. As a result, this region is considered a secondary centre of banana diversity (Baker and Simmonds, 1951; Shepherd, 1957; Karamura and Karamura, 1995).

2.5 The banana weevil, *Cosmopolites sordidus*

2.5.1 Origin and distribution

The banana weevil *Cosmopolites sordidus* Germer, 1824 (Coleoptera: Curculionidae), is a long snouted black beetle (10-16 mm) with a hard integument. *C. sordidus* probably originated in the Indo-Malaysian region from where Germar's specimens came (Zimmerman, 1968). Due to intercontinental travel by Europeans and Arabs, the weevil could have spread to many other countries in infested plants. *C. sordidus* is now known to be cosmopolitan, occurring in virtually all banana-growing countries of the world. In Africa, it was first reported in Uganda in 1910 (Gowdy, 1922) then in the Congo in 1913. It was later reported in Tanzania in 1922 and by 1936 it was reported in all banana-growing parts of Uganda. It is currently a serious pest in Uganda (Gold *et al.*, 1994a), Tanzania, Kenya (Reddy, 1989) and western DRC. Banana weevils are generally oligophagous, attacking only plants in the genera *Musa* and *Ensete*. Biotypes in *C. sordidus* are not yet known, but preliminary studies indicate that there are significant molecular differences among weevil populations from different countries (Ochieng, 1999).

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mulching, manure application and trapping of adult weevils to reduce populations. These practices, although available to peasant farmers, are very labour intensive, have not been well adopted and are thus less effective. Chemicals are effective but expensive as well as being dangerous to humans and the environment. Host plant resistance to banana weevil remains the most feasible, long-term control strategy for banana farmers in Africa.

2.6 Host plant resistance

Host plant resistance can be defined as the property that enables the host plant to avoid, tolerate, or recover from insect populations that would otherwise cause greater damage to other plants of the same species, under the same environmental conditions (Kogan, 1982; Thomas and Waage, 1996). However, sometimes host plant resistance may not refer to resistance properties of the plant itself but may be a result of other biotic and abiotic factors, for example, associations with other plants or with natural enemies of the insect pest. Hober (1980) referred to this type of resistance as non-functional resistance.

Plants and insects have coexisted for hundreds of thousands of years. Through evolution plants, both wild and cultivated, have developed a great diversity of mechanisms to deal with insect attack. Nevertheless it is difficult to come across a plant that does not harbour some insect pest (Frost, 1942). This means that phytophagous insects have developed mechanisms to overcome hurdles posed by host plants. This is sometimes reflected in an intricate host-finding and accepting process (Miller and Strikler, 1984). This process begins with dispersal of the insect, location of potential hosts, examination and acceptance of the host, then consumption of and/or oviposition on the host. Each activity in the sequence brings the insect into a situation in which an appropriate stimulus will lead to the next activity. These processes differ significantly from species to species. Ultimately host plant selection will lead an insect into choosing the right species of plant and selecting an individual plant within that species that is or will be suitable for feeding, survival and development (Bernays and Chapman, 1994).

Three classifications of resistance, which were first proposed by Painter (1951), are still widely used. In this classification resistance is divided into non-preference, antibiosis, and tolerance. It is important to note, though, that a resistance mechanism against a particular pest

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prospect of resistance breeding rather than simple selection and release, in the areas of Africa where these cultivars are important.

From a diagnostic survey conducted in Uganda, Gold *et al.* (1994a) found that plantains and EAHB were more susceptible to banana weevil attack than the other banana varieties which include Bogoya (Gros Michel, AAA) and the introduced cultivars Kisubi, Ndiizi (AB) and Kayinja (ABB). They also found that levels of susceptibility to weevils within highland bananas varied significantly among cultivars, with Nassaba and Kisansa showing twice as high damage scores as Mbwazirume and Nakyetengu. Degree of larval penetration into the corm was higher in Nakitembe, Namwezi and Musakala than the rest.

Speijer *et al.* (1993) showed that damage caused by banana weevil was higher on Gonja, a plantain used for roasting, and on Lusumba, a highland cooking banana, than on dessert cultivars (AAA). Sheshu-Reddy & Lubega (1993) showed that weevil survival was significantly different among EAHB highland cultivars, with cooking cultivars showing a little more susceptibility than brewing cultivars.

Fogain and Price (1994), working in Cameroon, screened a total of 52 varieties of *Musa* for weevil damage. Of these, plantains showed the highest susceptibility, while AAA bananas generally escaped attack. Ittyeipe (1986) mentioned that weevil infestation in Jamaica ranged from very high in plantains and medium for cultivar Cavendish, to very low in diploid (AA) cultivars. In Guadeloupe, a cultivar of the subgroup Pisang Awak showed high tolerance, despite heavy tunnelling (Pavis, 1991). In the same study, cultivar Yangambi-km5 was almost free of attack.

Some studies, however, are not in agreement with the bulk of literature available to date. For example in India, Viswanath (1981) found that ABB cultivars supported larval development more than AAB and AAA, or diploid cultivars, while in Puerto Rico, cultivar Laknau (an AAB) was resistant to weevils (Irizarry *et al.*, 1988). The apparent inconsistencies in response to weevil attack and damage found in the available literature (Table 2.1) may have resulted from working in different ecological conditions. These conditions present different biotic and abiotic factors, which influence host-plant interactions. There may also be a series of banana weevil biotypes, which have not yet been identified. The issue of biotypes complicates current work on screening, because it is not known whether there may be

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preference mechanisms in banana. Musabyimana (1995) found differential attraction of weevil adults to plants, but found no relationship between cumulative trappings and weevil damage indicated by Percentage Coefficient of Infestation (PCI) (Mitchell, 1978) on the same cultivar. This is supported by Abera *et al.* (1997) who did not find differences in plant attraction (based on trap catches) nor acceptance (based on oviposition levels) among three EAHB cooking, two EAHB brewing and Pisang Awak cultivars. Pavis and Minost (1993) found that there was no correlation between pseudostem attraction and infestation. They also indicated that resistant varieties were as attractive to weevils as susceptible ones, thus ruling out non-preference (antixenosis) as a resistance mechanism in bananas. This is supported by the fact that Ortiz *et al.* (1995) did not find a correlation between corm hardness and host plant resistance in segregating plantain progenies. They suggested that further investigations on banana resistance mechanisms should consider antibiosis as the possible mechanism of resistance.

Semio-chemicals are important in banana, as has been shown by the attraction of adult weevils to freshly cut plants and pseudostem traps. Studies have tried to determine the differences in attraction of weevils to semio-chemicals from different cultivars, but the results seem inconclusive. Budenberg *et al.* (1993) found that female weevils were equally attracted to freshly cut rhizomes of resistant and susceptible cultivars. They postulated that attraction by semio-chemicals from banana plants was for feeding rather than for oviposition, since weevils did not seem to be able to distinguish volatiles from the different cultivars they studied. Abera (1998), on the other hand, found similar oviposition on both susceptible and resistant cultivars. In another study, Rwekika (1996) found that the compound salicin (a phenolic glucoside) was a significant feeding attractant to banana weevils. Salicin was found to be present in higher quantities in the susceptible cultivars Githumo, Mbidde, Lusumba (EAHB) and Gonja (plantain). He also found that these susceptible cultivars had higher quantities of glucose. On the other hand, salicin was almost absent in the resistant cultivars Pisang Awak (ABB), Ndiizi (AB) and Kivuvu (ABB). Glucose was absent in Kivuvu and significantly lower in the other resistant cultivars. Rwekika (1996) therefore attributes resistance to the absence of feeding stimulants, mainly salicin and glucose. Another compound, 1,8-cineole, was identified as the active component of volatiles released from a known susceptible cultivar, Githumo (EAHB) in Kenya (Ndiege *et al.*, 1996).

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s been done on antibiosis in banana, yet many of the studies cited above rds antibiosis as the major resistance mechanism in banana and plantain. (1996) showed that Yangambi-km5 had a significant antibiotic effect on causing substantial mortality and lengthening of the developmental stages.) reported that egg and larval survival was significantly influenced by k, again hinting towards antibiosis as the possible resistance mechanism.

be an important biophysicaly mediated resistance mechanism to banana Minost (1993) found a negative correlation (r = -0.47) between corm l damage. Ortiz *et al.* (1995), however, did not find any relationship ctors in segregating plantain progenies. Hardness of the corm may e in larval development and may be an important resistance component in ntain cultivars. Latex has been found to be a defence mechanism against 'ants (Bonner & Galston, 1947), but no work in this respect has been anana. In Uganda, local farmers have observed that some cultivars with appeared resistant.

ve reported tolerance as a mechanism of resistance to banana weevil. size was recognised by Balachowsky (1963) as a resistance mechanism probably makes it able to tolerate attack, as larvae may not tunnel deep growing point. Large corms may also be able to tolerate many tunnels affecting their strength. To determine levels of tolerance to banana eed for long term studies to compare damage and yield loss among nis is because weevil populations and damage increase slowly and yield for a number of cycles (Rukazambuga *et al.*, 1998).

or banana weevil resistance

resistance genes from related banana species (wild and cultivated types) , sources of resistance must be identified. The genetics of resistance , gene action, and linkage to other characters may need to be studied.

Banana weevil resistance is unfortunately a complex trait and difficult to study, but complex resistance is more durable once released in a cultivar. Ortiz *et al.* (1995) found that it involves one or more incomplete or partially dominant resistance genes, coupled with a dosage effect at higher ploidy levels.

2.9.1 Conventional breeding

Crossbreeding programmes for improving banana and plantain have registered considerable successes in the last decade (Ortiz and Vuylsteke, 1996; Rowe and Rosales, 1993; Vuylsteke *et al.*, 1997). Breeding for resistance to banana weevil has, however, not featured prominently in any breeding programme. This is probably because of the absence of good sources of resistance and the lack of a simple screening method for weevil resistance, which would enable breeders to rapidly pinpoint resistance in the available germplasm.

Ortiz *et al.* (1995), using hybrids from Calcutta-4 (a wild diploid) and landrace plantain in West Africa, found that most of the diploid hybrids were resistant, while most of the polyploids were susceptible. Selections from this diploid population could make good parents for use in further crossings to attempt introgression of resistance into elite cultivars.

2.9.2 Genetic engineering

New techniques may be used to identify and generate resistance to banana weevil. Host plant resistance has often been difficult to determine and field-testing is cumbersome, time-consuming and expensive. From the literature available, results from screening studies have been ambiguous and inconsistent. As conventional breeding methods continue, it seems necessary to include some of the latest genetic engineering techniques. Three techniques are now available for banana genetic transformation. These include *Agrobacterium*-mediated transformation (May *et al.*, 1995), electroporation (Sagi *et al.*, 1994), and particle bombardment (Sagi *et al.*, 1995). These can be used to develop transgenic banana plants with resistance to the weevil. In other crop pests, resistance has been achieved through the expression of genes encoding toxins of the insecticidal bacterium *Bacillus thuringiensis*. Other proteins, such as protease inhibitors, have also been used in pest resistance (Frutos, 1993). Previous attempts to screen *B. thuringiensis* toxins against banana weevil did not yield

positive results and protease inhibitors may be more promising (Prof. Dirk de Waele[1], *personal communication*). Therefore, before *Musa* transgenics against banana weevil can be developed, there is a need to identify insecticidal proteins that are effective against the banana weevil. Crouch *et al.* (1998) believe that genetic engineering should be used as a supplement to conventional breeding methods by introducing unique and important genes into elite germplasm for use in further crossing.

2.10 Host plant resistance as an integrated pest management (IPM) component

Plant resistance to pests is a major component of integrated pest control, which aims at keeping pest populations below damaging levels. The method is most effective in pest populations that develop slowly (de Ponti, 1982). In Uganda, banana weevil population build-up is slow (Rukazambuga *et al.*, 1998). High oviposition and slow increase in population size suggests high (up to 80%) egg or larval mortality (Abera, 1998; Gold *et al.*, 1999c). This may suggest that antibiosis is one of the factors regulating population build-up and that it can be exploited in banana IPM strategies. The use of host plant resistance together with new IPM strategies like pheromone traps and biological control will go a long way in solving the weevil problem in banana cultures.

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CHAPTER III

EVALUATION OF HOST PLANT RESPONSE TO BANANA WEEVIL (*COSMOPOLITES SORDIDUS* GERMAR) IN *MUSA* GERMPLASM IN UGANDA

3.1 Introduction

Banana weevil is the most important insect pest of banana in Uganda and the whole East African region. It is threatening the banana crop on which millions of people depend for food and income. Since banana is a staple for about 7 million people in the region, and is grown mainly on a subsistence basis, it is important that an easily adoptable technology be found to solve the weevil problem. One way is to find resistance in the host plant, which in this case includes a highly diversified local germplasm, containing mainly the East African Highland banana (*Musa* AAA, 'Matooke' group). About 80 different banana cultivars have been identified by morphological characterisation and it is believed that the genetic diversity of the 'Matooke' group, which is yet to be investigated, is smaller (Karamura, 1998). Nevertheless it is still important to screen it for resistance to banana weevil. Together with the Matooke cultivars, people grow a series of other genotypes, which are considered exotic because they are of a more recent introduction. In the last five years some hybrids from a couple of breeding programmes have also been introduced and are currently being tested both at research centres and selected farmers fields.

To sustain banana and plantain production, a management strategy is required that would be easily available to resource poor farmers. Chemical control against the weevil is effective but expensive, contaminates the environment, and is poisonous to both humans and their domestic animals. Furthermore the development of weevil resistance to chemical pesticides has been documented (Collins *et al.*, 1991). A host of cultural control methods, which include field sanitation and removal of post harvest material have shown lack of adaptability since they require high labour, which again poor farmers cannot afford. The generation and provision of weevil resistant cultivars appears to be the best solution to the weevil problem, as resistant cultivars would be the cheapest technology available to poor farmers. However, very little work has been done on screening for banana weevil resistance and it still ranks as medium priority among banana breeders in the world (Huggan, 1993). The little information available

is fragmented, with a few cultivars screened in different countries. The results from these few studies are also not in agreement and have used genotypes, which may not be present in other countries making comparisons difficult. The objectives of this study therefore were to screen a representative sample of the endemic Matooke cultivars and a series of other *Musa* accessions in Uganda for resistance to banana weevil and to obtain some insight into resistance mechanisms that would be useful in a future breeding programme. The success of any breeding programme would centre on knowledge of the genetic importance and control of chosen weevil damage indices plus how these and other plant growth characteristics associate genetically.

3.2 Materials and Methods

3.2.1 Site

A field screening trial was established in November 1996 at the International Institute of Tropical Agriculture, East and Southern Africa Regional Centre (IITA-ESARC), located at Namulonge, Uganda. Namulonge (00.53N, 32.58E), is 25 km north east of Kampala and 1,150 m above sea level. It has dark, reddish brown, loamy soil with a pH ranging from 5.4 to 6.4. Mean annual rainfall is 1,200 mm with bimodal distribution. The two rain seasons are March to June and September to December (Yost and Eswaran, 1990). Average daily temperatures are 17.5 °C minimum and 27 °C maximum (Gold *et al.*, 1998). The conditions at Namulonge are representative of the majority of banana growing areas in Uganda. Wricke and Weber (1986), recommend that that for successful estimation of genetic variances and covariances in a vegetatively propagated species, at one environment, the test plants must be grown under conditions that simulate the conditions in practice as much as possible.

3.2.2 Experimental design

The germplasm included representative samples from all five clonal groups of the East Africa Highland bananas (EAHBs) (*Musa* AAA-EA), plantains (*Musa* AAB), exotic cooking and brewing cultivars (*Musa* ABB), desert cultivars (*Musa* AAA), diploids (*Musa* AA and AB) and selected *Musa* hybrids. Again Wricke and Weber (1986) recommend that the diversity of the clones selected must be high and well representative of the species. The clones selected for this study were highly diverse both in their genomic origin and end use (Table 3.1).

Table 3.1. Information on *Musa* accessions used in the study ([1] Parents of hybrids are female x male)

Cultivar	Genome group or Parents[1]	Sub-group	Local Use
Atwalira	AAA	EAHB-Matooke	Cooking
Bagandeseza	AAA	EAHB-Matooke	Cooking
Bluggoe	ABB	Bluggoe	Cooking
Bogoya	AAA	Gros Michel	Dessert
Bukumu	AAA	EAHB-Matooke	Cooking
Cavendish	AAA	Cavendish	Dessert
Calcutta-4	AA	Wild banana	None
Endiirira	AAA	EAHB-Matooke	Brewing
Enshenyi	AAA	EAHB-Matooke	Cooking
FHIA03	AABB	Banana hybrid	Brewing and dessert
Gonja	AAB	Plantain	Roasting and cooking
Kabula	AAA	EAHB-Beer	Brewing
Kayinja	ABB	Pisang Awark	Brewing and juice
Kibuzi	AAA	EAHB-Matooke	Matooke
Kisansa	AAA	EAHB-Matooke	Matooke
Kisubi	AB	Nay Poovan	Brewing and juice
Mbwazirume	AAA	EAHB-Matooke	Cooking
Musakala	AAA	EAHB-Matooke	Cooking
Mutangendo	AAA	EAHB-Matooke	Cooking
Nakabululu	AAA	EAHB-Matooke	Cooking
Nakamali	AAA	EAHB-Matooke	Cooking
Nakawere	AAA	EAHB-Matooke	Cooking
Nakitembe	AAA	EAHB-Matooke	Cooking
Nakyetenbe	AAA	EAHB-Matooke	Cooking
Nalukira	AAA	EAHB-Beer	Brewing
Namafura	AAA	EAHB-Matooke	Cooking
Naminwe	AAA	EAHB-Matooke	Cooking
Namwezi	AAA	EAHB-Matooke	Cooking
Nandigobe	AAA	EAHB-Matooke	Cooking
Ndibwabalangira	AAA	EAHB-Matooke	Cooking
Ndiizi	AB	Ney Poovan (Apple banana)	Dessert
Nsowe	AAA	EAHB-Beer	Brewing
Obino l'Ewai	AAB	Plantain	Roasting and cooking
Shombobuku	AAA	EAHB-Beer	Brewing
Siira	AAA	EAHB-Matooke	Cooking
Tereza	AAA	EAHB-Matooke	Cooking
TMB2x6142-1	Nyamwihongora x Long Tavoy	EAHB-Hybrid (2X)	-
TMB2x7197-2	SH 3362 x Long Tavoy	Banana hybrid (2X)	-
TMB2x8075-7	SH 3362 x Calcutta 4	Banana hybrid (2X)	-
TMBx612-74	Bluggoe x Calcutta-4	Banana hybrid (4X)	-
TMPx15108-6	TMPx 4479-1 x SH 3362	Plantain hybrid (3X)	-
TMPx5511-2	Obino l'Ewai x Calcutta 4	Plantain hybrid (4X)	-
TMPx7002-1	Obino l'Ewai x Calcutta 4	Plantain hybrid (4X)	-
TMPx7152-2	Mbi Egome 1 x Calcutta 4	Plantain hybrid (4X)	
Yangambi-km5	AAA	-	Dessert

A 126 m x 36 m trial was planted at the IITA-ESARC Sendusu farm in Namulonge. Forty-five *Musa* accessions collected from the National Banana Research Programme (NBRP) germplasm collection, surrounding villages, and IITA-ESARC germplasm collection, were planted in a randomised block design, with 12 blocks (one plant per block per cultivar). The susceptible cultivar Atwalira was used for border plants in order to increase and evenly distribute weevil infestation levels the blocks were separated by lines of the same cultivar. Sword suckers were used as planting material and before planting suckers were pared to remove the outermost tissue which may contain weevil eggs, larvae and parasitic nematodes. The pared suckers were then dipped in hot water (55-60°C) for 20 minutes, left to cool and then planted in the field. Hot water treatment is a recommended practice to ensure that weevil eggs, larvae and parasitic nematodes that may have escaped the paring are killed, thereby ensuring clean planting material. Planting holes, 60 cm in diameter and 60 cm deep were dug at a spacing of 3 m by 2 m. At planting 250 g of single super phosphate (SSP) fertiliser was mixed with some soil and then the sucker was placed inside the hole and covered with topsoil. Use of SSP at planting is another recommendation to help the plant quickly establish by inducing rapid development of roots. Gap filling (replanting where plants failed to establish) was done twice, *i.e.* January and April 1997.

3.2.3 Weevil infestation

Adult weevils collected from farmers' fields and maintained in the laboratory were marked to distinguish them from other weevils that may immigrate from neighbouring plots and new weevils, which will develop in the plants. The marking was done by scratching a mark diagonally to the left across the thorax using a scalpel (Figure 3.1). Ten weevils (five female and five males) were released at the base of each mat in the evening (after 18:00 hours). This timing is important since weevils are nocturnal and can be killed by high day temperatures.

Figure 3.1. Adult banana weevil marked by scratching a diagonal mark on the thorax, using a scalpel

3.2.4 Weevil damage assessment

Banana weevil damage assessment was conducted at harvest when the bunch begins to ripen. Data on percentage coefficient of infestation (PCI) (Mitchell, 1978; Gold *et al.*, 1994a; Rukanzambuga *et al.*, 1998) was obtained by scoring presence/absence of damage in each of ten 18° sections guided by a metal template placed against the corm (Figure 3.2a). This was done for two positions on the corm, *i.e.* 5 cm from the collar (upper position) and 10 cm from the collar (lower position). The collar is a clear separation line between the pseudostem and the corm. PCI scores generally ranged from 0 to 60 (Figure 3.3). Peripheral damage was also assessed by estimating the percentage of the corm periphery visually covered with weevil galleries (*Gold et al.* 1994b)

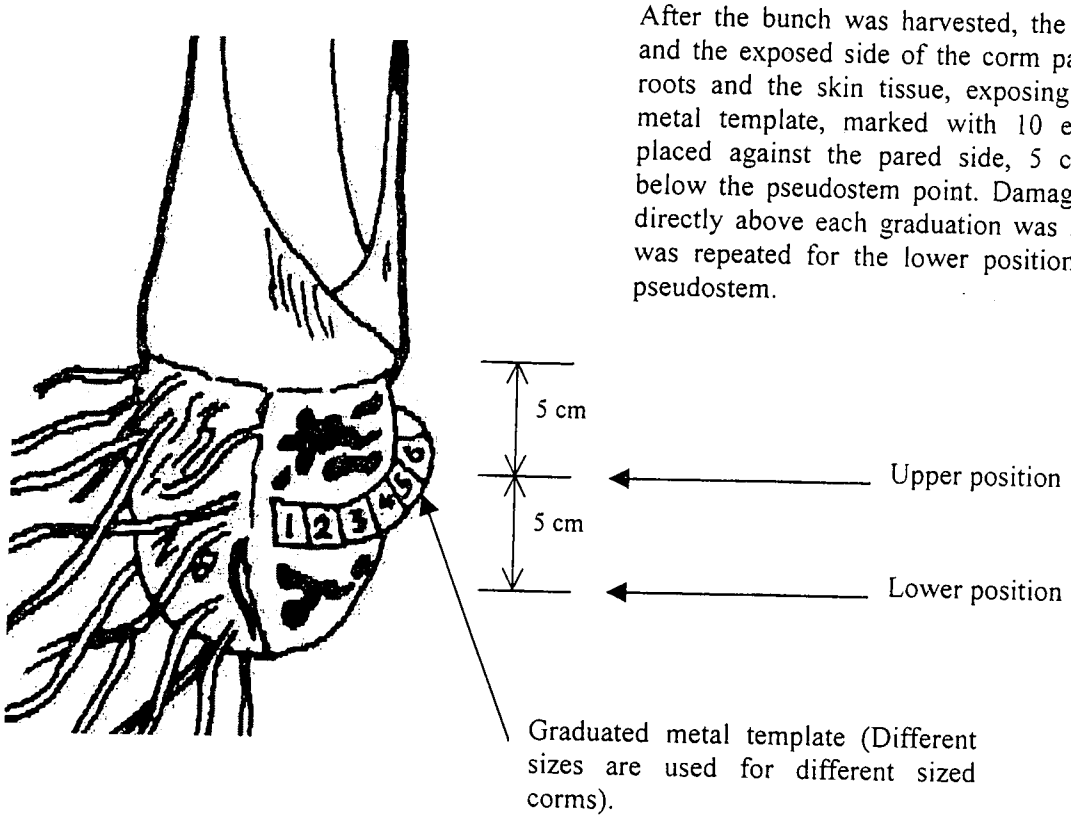


Figure 3.2a. Weevil damage assessment- scoring for Percentage Coefficient of Infestation (PCI)

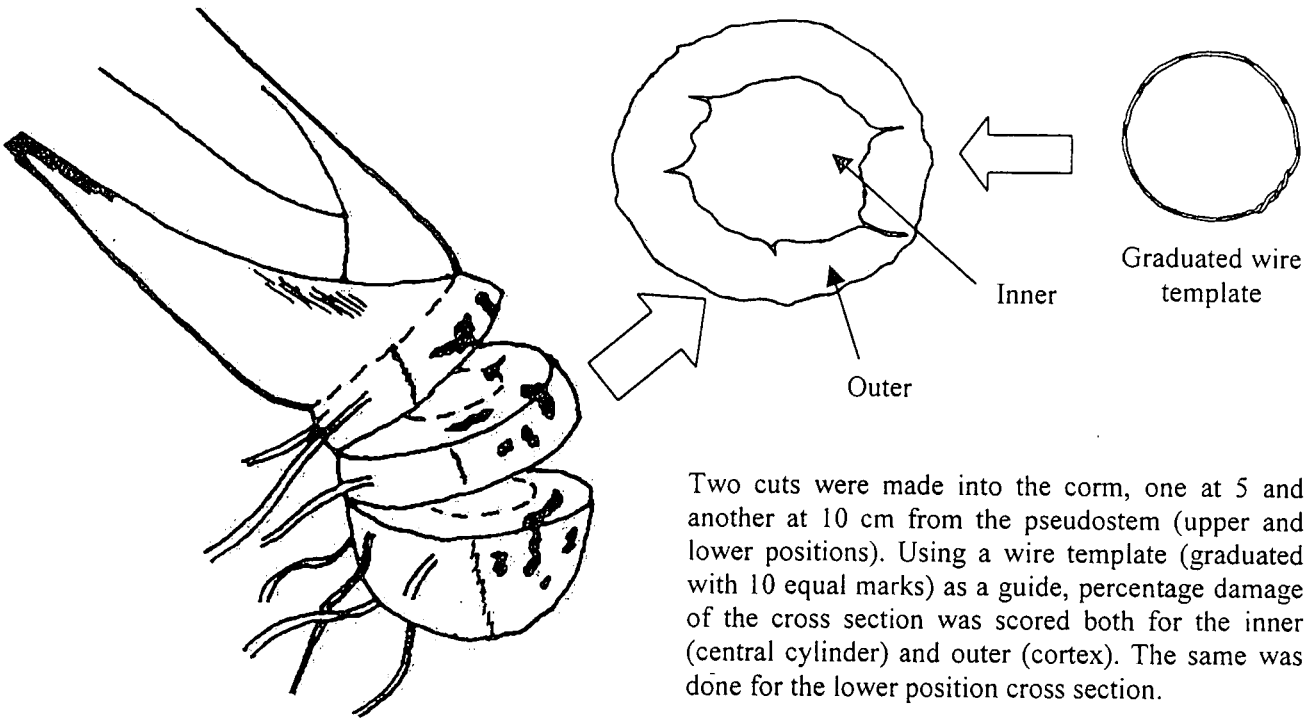
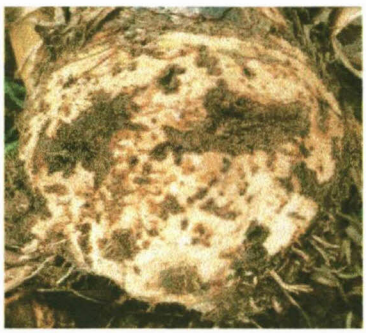


Figure 3.2b. Weevil damage assessment – scoring cross section inner (XI) and cross section outer (XO) damage

Two cross sections were made; at 5 cm (upper position) and 10 cm (lower position) below the pseudostem. For each cross section, weevil damage was assessed for the central cylinder (inner) and the cortex (outer) of the corm by estimating the percentage of corm area with larval galleries, guided by a wire template with 10 divisions marked on the wire (Figure 3.2b). Data was also taken for inner and outer diameter of the corm.

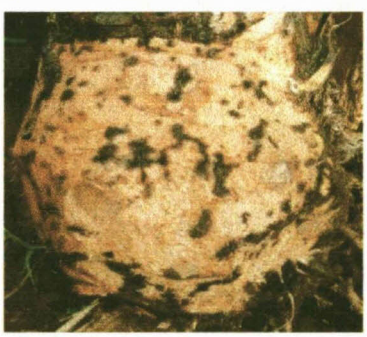
After scoring PCI, XI and XO, corm hardness (inner and outer) was measured using a hand held digital penetrometer (Digital Force Gauge, Model: S/N 25160, John Chatillon and Sons Inc., North Carolina, USA), by pushing the penetrometer into three randomly selected points each for the inner and outer sections of the corm and the mean for each was used for analysis.

60%



30%

10%



5%

0%

Figure 3.3. Indication of approximate percentage weevil damage

Dry matter content (inner and outer) was established by randomly collecting three equal sized pieces of inner and outer corm tissue. The pieces were weighed to determine wet weight and then dried in a laboratory oven, where after the constant dry weight was also recorded. Dry matter content was taken as the ratio of the mean wet and dry weight. Resin/sap production was scored on a maiden sucker in nine of the best blocks, by first paring the corm of a standing plant and after 24 hours counting the number of droplets per square centimetre at three randomly selected positions of the pared area. Other growth parameters like days to flowering and days to harvest were also recorded during the same period. Table 3.2 shows all the collected and derived parameters.

3.2.5 Data analysis

3.2.5.1 Basic statistics

Data were tested for normality and found to be relatively normally distributed necessitating no transformation. Then, it was exposed to analysis of variance using the PROC GLM procedure in Statistical Analysis System (SAS) software (SAS Institute, 1991). Means were separated using the least significant difference (LSD) test and all the variables of data collected were subjected to Pearson's correlations. The analyses were divided into three parts, (i) with all the cultivars included, (ii) with only EAHBs and (iii) with exotic (all other types excluding the local EAHBs) cultivars only.

3.2.5.2 Multivariate analysis

The objectives of using multivariate methods were twofold. First, to be able to put together all the different weevil damage variables and partition the cultivars into susceptible, intermediate and resistant groups or clusters, by using cluster analysis, and secondly, to eliminate redundancy in data, because all the weevil damage variables were highly correlated.

Cluster analysis was performed using the 'k-means clustering' procedure in STATISTICA (StatSoft, 1995). This procedure which is non-hierarchical, produces a pre-set number of clusters (in this case three) with the highest possible distinction, while minimising the variance within

Table 3.2. Characters and measurements considered in this study

Characters of weevil damage interest

1. Percentage Coefficient of Infestation (PCI) (Upper position)
2. Percentage Coefficient of Infestation (PCI) (Lower position)
3. Percentage damage - The total of PCI upper and PCI lower
4. Inner cross section damage (Upper)
5. Outer cross section damage (Upper)
6. Inner cross section damage (Lower)
7. Outer cross section damage (Lower)
8. Coefficient of infestation, a visual assessment of weevil damage
9. Percentage inner damage - The mean of inner cross-section upper and lower
10. Percentage outer damage - The mean of outer cross section upper and lower
11. Total damage - The mean of inner and outer cross section of the upper and lower positions

Characters of agronomic interest

12. Suckering ability
13. Number of days from planting to flowering
14. Number of days from flowering to harvest
15. Bunch weight
16. Plant height at flowering
17. Plant girth (at 100 cm) at flowering
18. Number of leaves at flowering

Characters of botanical/structural interest

19. Inner diameter of the corm (Upper)
20. Outer diameter of the corm (Upper)
21. Inner diameter of the corm (Lower)
22. Outer diameter of the corm (Lower)
23. Peripheral corm hardness
24. Outer corm hardness
25. Inner corm hardness
26. Outer dry matter content (XO) - The ratio of the wet to the dry weight of the cortex
27. Inner dry matter content (XI) - The ratio of the wet to the dry weight X 100 of the central cylinder
28. Resin/sap content

each cluster. It uses repeated analysis of variance and iteration (Aldenderfer and Blashfield, 1984; Smith, 1990).

Principle component analysis (PCA) also restructures data containing many correlated variables into smaller sets of components of the original variables. The sets do not correlate with each other, but the components within each set are highly correlated. So the sets become new variables and can be used for uni-variate analysis (Smith, 1990; Iezzoni and Pritts, 1991; Ssango, 1998).

PCA was performed on the three damage observations (Total damage, PCI, XI and XO) of the 45 *Musa* accessions to reveal patterns within the data matrix using SAS software (SAS Institute, 1991). First and second principle component (PC1 and PC2) axis values were plotted to enhance dispersion of the host response to banana weevil infection of the *Musa* accessions.

In both multivariate analyses (cluster analysis and PCA), four variables *i.e.* percentage cross section damage on the inner (central cylinder) (XI), cross section damage on the outer (cortex) (XO), coefficient of infestation (PCI) and total inner damage (TD) were used together because they are highly correlated and important damage indicators. Cross section damage variates indicate how deep the weevil larvae can penetrate into the corm. Such damage would be important in affecting nutrient and water uptake by the plant, thus affecting yield and eventually plantation life.

3.2.5.2 Quantitative genetic analysis

Estimates of clonal heritabilities and genetic correlations for all the variable measures were calculated in order to shed some light on the genetic control of key weevil resistance traits plus their genetic relationships for better resistance selection. The data was subjected to MANOVA option in SAS software (SAS Institute, 1991). Genetic variances were obtained by using the formula of Burton and DeVane (1953) and Wricke and Weber (1986):

$$\sigma^2_{clone} = \frac{MS_{clones} - MS_{error}}{\sigma^2_{error}}$$

Where MS_{clone} and MS_{error} are the mean squares for clones and errors respectively. σ^2_{error} is the total error variance. According to Burton and DeVane (1953), this method has two advantages for calculating genetic variance in clonal material. First, it does not depend on the assumption that the environmental variance is the same for segregating and non-segregating populations, and second it appreciably reduces the amount of GxE interaction, especially when working in one environment. It is important to note, though, that such computations of genetic variance (plus other estimates, which depend on this estimate) are often over-estimated. This is because one cannot separate variance due to dominance and epistasis (Burton and DeVane, 1953). Clonal heritability (in the broad sense) estimates were computed for each variable, using the formula of Burton and DeVane (1953), Hanson (1963) and Anido *et al.* (1998):

$$h^2 = \frac{\sigma^2_{clone}}{\sigma^2_{clone} + \sigma^2_e}$$

Where σ^2_{clone} is the variance component due to the clone (clonal variance) and σ^2_e the variance due to error. From each variable's analysis of variance, the cross product sum matrix was used to calculate covariances and then genetic correlation between the characters using the formulae below (Searle, 1961; Scossiroli *et al.*, 1963; Burdon and Apiolaza, 1998):

$$r_g = \frac{COV_{AB}}{\sqrt{\sigma^2_A \, x \, \sigma^2_B}}$$

Where Cov_{AB} is the covariance between characters A and B divided by the square root of the product of their genetic variances.

3.3 Results

3.3.1 Basic statistics

In all the results from the several analyses, total inner damage, which is a mean of all the four inner damage scores, was used as the most important criteria for selecting resistance and for

ranking cultivars. This is because it measures the extent to which weevil larvae can penetrate deep into the corm. Damage that occurs deep inside the corm therefore translates directly into yield loss and diminished survival of the plant. Percentage coefficient of infestation (PCI) has also been included in the result tables, as it measures a different dimension to the issue of weevil damage. It quantifies damage on the periphery of the corm and although such damage does not extend deep, it to a certain extent influences root development, because the tissue from which roots originate becomes necrotic leading to root death.

There were significant differences among the cultivars studied in their response to banana weevil damage. Table 3.3 shows the response of all cultivars screened for four important damage indices, total inner damage ranged from 9.9 to 0.1 while percentage coefficient of infestation ranged from 19.8 to 0.5. The cultivar names are ranked using the total damage variable and overall Ndiibwabalangira ranked as the most susceptible. It was, however, not significantly different from the cultivars listed up to Nakamali. These could probably be described as the most susceptible of the cultivars tested. Two banana hybrids, TMB2x6142-1 and TMB2x7197-2 at the bottom of the list have Long Tavoy as their male parent. Long Tavoy may be the origin of resistance genes, since the female parents are known to be susceptible. Yangambi-km5 is the most resistant cultivar followed by Kisubi, Cavendish, FHIA03, and Kayinja. Unfortunately these are exotic to Uganda and are grown for other uses other than food (see Table 3.1). Mbwazirume and Tereza are local landraces with the lowest total inner damage. However, when PCI was considered, Gonja, a plantain, shows the highest damage levels, followed by TMPx5511-2 (a plantain hybrid) and Obino l'Ewai, a West African local plantain landrace. From some literature it will be noted that plantains are ranked most susceptible. This difference in rank order is because this is the first time total inner damage (other than PCI) has been used as a criteria for ranking cultivars. If PCI had been used, as a ranking criteria in this study, Gonja would be most susceptible, followed by TMPx5511-2 (a plantain hybrid), Obino l'Ewai, Nsowe and Ndiibwabalangira. In contrast, when using total inner damage as criteria, Nsowe shows quite low inner damage and has been ranked as resistant.

Table 3.4 shows the response of EAHBs when analysed separately. Ndiibwabalangira was once again the most susceptible, but was not significantly different from the other cultivars listed up to Enshenyi. Mbwazirume and Tereza were the two least damaged local cooking bananas.

Table 3.3. Means (± standard error) of banana weevil damage variables for *Musa* cultivars in Uganda

Name	Total damage	% Inner damage	% Outer damage	% Coefficient of infestation (PCI)
Ndiibwabalangira	9.9±3.2	10.2±4.5	9.5±2.2	19.8±2.9
Endiirira	9.0±3.4	8.2±3.6	9.9±3.4	19.4±4.3
Kibuzi	8.5±3.2	7.3±4.3	9.8±2.1	17.0±2.3
Naminwe	8.1±2.7	7.8±3.3	8.5±2.1	18.9±4.3
Obino l'Ewai	8.1±1.6	4.8±1.5	11.3±1.9	19.9±2.6
TMPx5511-2	7.9±2.1	4.9±2.7	10.9±1.7	20.6±2.1
Nakawere	7.9±3.6	6.9±4.4	8.9±2.7	17.4±4.5
Namafura	7.7±2.5	5.7±2.7	9.7±2.4	19.8±3.3
Gonja	7.5±1.7	6.2±2.2	8.8±1.6	22.6±3.6
TMPx7152-2	7.3±1.2	3.8±0.9	10.7±1.8	17.9±2.5
Atwalira	7.0±2.0	4.3±1.9	9.6±2.3	18.2±3.2
Nakabululu	6.8±1.8	4.4±1.8	9.3±1.9	18.0±2.7
Musakala	6.5±2.4	4.7±2.3	8.2±2.6	18.2±2.5
Nakitembe	6.4±2.0	6.0±2.4	6.9±1.6	17.8±2.9
Shombobuleku	6.3±3.0	5.3±3.9	7.4±2.3	14.7±2.9
TMPx7002-1	6.3±1.6	4.8±1.7	7.8±1.7	14.0±2.3
Bagandeseza	6.1±2.2	5.1±2.8	7.1±2.1	16.5±3.3
Kisansa	6.0±1.2	3.3±1.2	8.6±1.3	18.9±1.9
Nakamali	5.9±2.3	5.8±3.1	6.0±1.7	11.3±2.1
Namwezi	5.8±1.7	6.0±2.1	5.7±1.4	14.0±2.1
Enshenyi	5.7±1.6	5.1±2.9	6.3±0.9	15.2±2.1
Nandigobe	5.2±2.8	4.3±3.8	6.0±1.8	16.2±2.3
Mutangendo	5.0±0.9	2.3±0.8	7.7±1.1	14.9±1.9
Kabula	5.0±2.3	4.8±3.8	5.1±0.9	13.7±1.7
Siira	4.8±0.8	2.7±1.0	6.8±1.0	15.5±1.8
Bluggoe	4.1±2.0	2.9±2.1	5.4±2.0	11.5±3.0
Nakyetengu	4.1±1.4	3.0±1.6	5.2±1.4	10.7±1.6
Bogoya	4.0±1.5	1.9±1.2	6.0±1.8	14.7±2.5
Bukumu	3.9±0.8	2.1±0.7	5.8±1.1	14.2±1.7

Table 3.3. Means (± standard error) of banana weevil damage variables for *Musa* cultivars in Uganda (continued)

Name	Total damage	% Inner damage	% Outer damage	% Coefficient of infestation (PCI)
Nsowe	3.3±0.6	0.6±0.3	6.0±1.2	19.9±2.6
Ndiizi	3.1±0.7	0.4±0.1	5.9±1.3	12.6±2.2
Nalukira	3.1±1.2	1.8±1.4	4.4±1.1	10.1±1.6
Tereza	2.7±0.5	1.2±0.5	4.2±0.6	13.6±0.5
Mbwazirume	2.7±0.5	0.7±0.3	4.6±0.7	11.6±1.0
Kayinja	2.3±1.2	1.8±1.3	2.8±1.2	9.9±2.8
FHIA03	1.9±0.6	0.0±0.0	3.7±1.2	8.7±2.6
Cavendish	1.8±0.6	0.2±0.2	3.4±1.1	8.2±1.9
TMPx15108-6	1.7±0.7	0.5±0.4	2.9±0.9	6.9±1.6
TMBx612-74	1.4±0.6	0.5±0.4	2.3±0.8	6.8±2.1
Kisubi	1.0±0.4	0.1±0.1	1.8±0.8	7.5±2.4
Yangambi KM5	0.4±0.2	0.1±0.1	0.6±0.4	2.3±1.3
TMB2x8075-7	0.3±0.1	0.0±0.0	0.5±0.2	2.9±1.2
Calcutta-4	0.2±0.1	0.0±0.0	0.4±0.3	1.3±0.4
TMB2x7197-2	0.2±0.1	0.1±0.1	0.3±0.2	0.7±0.5
TMB2x6142-1	0.1±0.1	0.0±0.0	0.2±0.1	0.5±0.5
LSD (P=0.05)	*4.0*	*5.0*	*3.5*	*5.3*

In our interviews, Ugandan farmers reported that the brewing type bananas, which produce more sap, are generally resistant. This is probably the reason why Nsowe and Nalukira showed the least damage, as indicated by their ranking on the list (Table 3.4). It is important to note that Nsowe, although scoring low for inner damage has the highest PCI among EAHBs. In the field it has been noticed that Nsowe is heavily damaged in the pseudostem, unlike any other cultivars. This could be a form of tolerance. Three other beer cultivars, Endiirira, Shombobureku and Bagandeseza are, however, higher up in the list and do not show resistance as Nsowe and Nalukira.

Table 3.4. Means (± standard error) of banana weevil damage variables for East African Highland banana (EAHB) cultivars in Uganda (*=Brewing types)

Name	Total damage	% Outer damage	% Inner damage	% Coefficient of Infestation
Ndiibwabalangira	9.9±3.2	10.2±4.5	9.5±2.2	19.8±2.9
Endiirira*	9.0±3.4	8.2±3.6	9.9±3.4	19.4±4.3
Kibuzi	8.5±3.2	7.3±4.3	9.8±2.1	17.0±2.3
Naminwe	8.1±2.7	7.8±3.3	8.5±2.1	18.9±4.3
Nakawere	7.9±3.6	6.9±4.4	8.9±2.7	17.4±4.5
Namafura	7.7±2.5	5.7±2.7	9.7±2.4	19.8±3.3
Atwalira	7.0±2.0	4.3±1.9	9.6±2.3	18.2±3.2
Nakabululu	6.8±1.8	4.4±1.8	9.3±1.9	18.0±2.7
Musakala	6.5±2.4	4.7±2.3	8.2±2.6	18.2±2.5
Nakitembe	6.4±2.0	6.0±2.4	6.9±1.6	17.8±2.9
Shombobuleku*	6.3±3.0	5.3±3.9	7.4±2.3	14.7±2.9
Bagandeseza*	6.1±2.2	5.1±2.8	7.1±2.1	16.5±3.3
Kisansa	6.0±1.2	3.3±1.2	8.6±1.3	18.9±1.9
Nakamali	5.9±2.3	5.8±3.1	6.0±1.7	11.3±2.1
Namwezi	5.8±1.7	6.0±2.1	5.7±1.4	14.0±2.1
Enshenyi	5.7±1.6	5.1±2.9	6.3±0.9	15.2±2.1
Nandigobe	5.2±2.8	4.3±3.8	6.0±1.8	16.2±2.3
Mutangendo	5.0±0.9	2.3±0.8	7.7±1.1	14.9±1.9
Kabula*	5.0±2.3	4.8±3.8	5.1±0.9	13.7±1.7
Siira	4.8±0.8	2.7±1.0	6.8±1.0	15.5±1.8
Nakyetengu	4.1±1.4	3.0±1.6	5.2±1.4	10.7±1.6
Bukumu	3.9±0.8	2.1±0.7	5.8±1.1	14.2±1.7
Nsowe*	3.3±0.6	0.6±0.3	6.0±1.2	19.9±2.6
Nalukira*	3.1±1.2	1.8±1.4	4.4±1.1	10.1±1.6
Tereza	2.7±0.5	1.2±0.5	4.2±0.6	13.6±0.5
Mbwazirume	2.7±0.5	0.7±0.3	4.6±0.7	11.6±1.0
LSD (P=0.05)	*4.6*	*5.8*	*3.9*	*5.8*

Table 3.5. Means (± standard error) of banana weevil damage variables for *Musa* cultivars exotic to Uganda, and hybrids

Name	Total damage	% Outer damage	% Inner damage	% Coefficient of Infestation (PCI)
Obino l'Ewai	8.1±1.6	11.3±1.9	4.8±1.5	19.9±2.6
TMPx5511-2	7.9±2.1	10.9±1.7	4.9±2.7	20.6±2.1
Gonja	7.5±1.7	8.8±1.6	6.2±2.2	22.6±3.6
TMPx7152-2	7.3±1.2	10.7±1.8	3.8±0.9	17.9±2.5
TMPx7002-1	6.3±1.6	7.8±1.7	4.8±1.7	14.0±2.3
Bluggoe	4.1±2.0	5.4±2.0	2.9±2.1	11.5±3.0
Bogoya	4.0±1.5	6.0±1.8	1.9±1.2	14.7±2.5
Ndiizi	3.1±0.7	5.9±1.3	0.4±0.1	12.6±2.2
Kayinja	2.3±1.2	2.8±1.2	1.8±1.3	9.9±2.8
FHIA03	1.9±0.6	3.7±1.2	0.0±0.0	8.7±2.6
Cavendish	1.8±0.6	3.4±1.1	0.2±0.2	8.2±1.9
TMPx15108-6	1.7±0.7	2.9±0.9	0.5±0.4	6.9±1.6
TMBx612-74	1.4±0.6	2.3±0.8	0.5±0.4	6.8±2.1
Kisubi	1.0±0.4	1.8±0.8	0.1±0.1	7.5±2.4
Yangambi KM5	0.4±0.2	0.6±0.4	0.1±0.1	2.3±1.3
TMB2x8075-7	0.3±0.1	0.5±0.2	0.0±0.0	2.9±1.2
Calcutta-4	0.2±0.1	0.4±0.3	0.0±0.0	1.3±0.4
TMB2x7197-2	0.2±0.1	0.3±0.2	0.1±0.1	0.7±0.5
TMB2x6142-1	0.1±0.1	0.2±0.1	0.0±0.0	0.5±0.5
LSD (P=0.05)	*2.9*	*3.6*	*2.8*	*4.7*

These cultivars have been observed to regularly revert into cooking clone types (Deborah Karamura[2], *personal communication*). Therefore, not all EAHB brewing types are resistant as was thought to be the case. Table 3.5 shows the response of cultivars exotic to Uganda, analysed separately. Obino l'Ewai showed the highest susceptibility to banana weevil damage, but was not significantly different from the other cultivars listed up until TMPx7002-1, as shown in the

[2] *National Banana Research Programme, Kawanda Agricultural Research Institute, P.O. Box 7065, Kampala, Uganda. Email: dkaramura@kari.go.ug*

table. Note that Gonja showed the highest PCI, while hybrids TMB2x6142-1 and TMB2x7197-2, showed highest resistance overall with all damage indices almost zero.

Several workers have reported plantains (AAB) as being the most susceptible *Musa* cultivars to banana weevil (Chapter II). In this study, when data was analysed by genome groups (Table 3.6), plantains ranked highest for all damage variables but none was significantly different. As expected, wild banana Calcutta-4 (AA) showed the least total damage.

Table 3.6. Means (± standard error) of banana weevil damage variables by genome groups of *Musa* in Uganda

Genome group	Total damage	% Inner damage	% Outer damage	% Coefficient of infestation (PCI)
AAB	7.8±1.1	5.5±1.3	10.0±1.2	21.3±2.2
AAA-EA	5.9±0.4	4.6±0.5	7.2±0.4	16.0±0.5
ABB	3.3±1.2	2.4±1.3	4.3±1.2	10.8±2.0
HYBRIDS	2.9±0.5	1.6±0.4	4.3±0.6	8.7±0.9
AB	2.4±0.5	0.3±0.1	4.4±1.0	10.8±1.7
AAA	1.8±0.5	0.6±0.3	3.0±0.7	7.5±1.4
AA	0.2±0.1	0.0±0.0	0.4±0.3	1.3±0.4
LSD (P=0.05)	*4.1*	*5.0*	*3.7*	*5.8*

3.3.2 Cluster analyses

A non-hierarchical clustering method was used to cluster all the cultivars into three response groups, *i.e.* resistant, intermediate and susceptible. Table 3.7a shows all the cultivars studied grouped into the three different clusters. Most of the cultivars, including all plantains, were grouped in the susceptible cluster although a good number were also intermediately resistant. The mean values of the damage variables for each cluster are shown in Table 3.7b.

Table 3.7a. Three response groups derived from cluster analysis of all *Musa* cultivars together

RESISTANT (Cluster 1)		INTERMEDIATE (Cluster 2)		SUSEPTIBLE (Cluster 3)	
Name	Total damage	Name	Total damage	Name	Total damage
TMPx15108-6	2.0	Nakamali	6.4	TMPx7152-2	10.7
Cavendish	1.7	Enshenyi	5.5	Kibuzi	10.1
Tmbx612-74	1.4	Kabula	5.4	Ndiibwabalangira	9.9
Kisubi	1.0	Siira	5.2	Endiirira	9.2
Yamgambi KM5	0.3	Nandigobe	5.2	Nakawere	8.8
TMB2x8075-7	0.3	Mutangendo	4.9	Obino l'Ewai	8.3
Calcutta-4	0.2	Bukumu	4.9	TMPx5511-2	7.9
TMB2x7197-2	0.1	Nakyetengu	4.1	Namafura	7.7
TMB2x6142-1	0.1	Bluggoe	4.0	Atwalira	7.7
		Bogoya	3.7	Namwezi	7.6
		Nsowe	3.3	Naminwe	7.6
		Mbwazirume	3.1	Gonja	7.3
		Nalukira	3.1	TMPx7002-1	6.8
		Tereza	3.0	Musakala	6.5
		Ndiizi	2.9	Nakabululu	6.4
		Kayinja	2.4	Shombobureku	6.4
		FHIA03	2.2	Nakitembe	6.2
				Bagandeseza	6.1
				Kisansa	5.8

Table 3.7b. Mean values (± standard deviation) of the three important variables for the respective clusters in Table 3.7a above

Cluster	PCI	Inner damage	Outer damage	Total damage
Resistant	4.1±3.2	0.2±0.3	1.3±1.2	0.8±0.7
Intermediate	13.4±2.7	2.5±1.7	5.6±1.1	4.1±1.2
Susceptible	18.4±2.0	6.3±2.0	9.2±1.6	7.7±1.4

Table 3.8a. Three response groups derived from cluster analysis of EAHB cultivars only ranked on descending damage levels (*=brewing types)

Resistant	Intermediate	Susceptible
Mbwazirume	Bagandesesa*	Atwalira
Nakyetengu	Enshenyi	Endiirira*
Mutangendo	Kabula*	Kibuzi
Nsowe*	Kisansa	Naminwe
Nalukira*	Bukumu	Nakawere
Tereza	Musakala	Ndiibwabalangira
	Nakabulu	Namafura
	Nakamali	
	Nakitembe	
	Namwezi	
	Nandigobe	
	Shombobureku*	
	Siira	

Table 3.8b. Mean values (± standard deviation) of three key variables for the respective response clusters in Table 3.8a above

Cluster	PCI	Inner damage	Outer damage	Total damage
Resistant	13.8±3.5	1.7±0.9	5.5±1.2	4.0±0.8
Intermediate	15.9±1.8	4.8±1.4	7.2±0.9	6.0±0.7
Susceptible	19.3±0.6	7.6±2.0	9.8±0.9	8.7±1.1

Table 3.9a. Three response groups derived from cluster analysis using *Musa* cultivars exotic in Uganda ranked on descending damage levels.

Resistant	Intermediate	Susceptible
Yangambi-km5	Cavendish	TMPx7152-2
Calcutta-4	TMPx15108-6	Gonja
TMB2x6142-1	Ndiizi	Obino l'Ewai
TMB2x8075-7	Kayinja	TMPx5511-2
TMB2x7197-2	Kisubi	TMPx7002-1
	Bogoya	
	Bluggoe	
	TMBx612-74	
	FHIA03	

Table 3.9b. Mean values (± standard deviation) of three key variables for three respective clusters in Table 3.9a above

Cluster	PCI	Inner damage	Outer damage	Total damage
Resistant	1.5±0.9	0.0±0.0	0.4±0.2	0.2±0.1
Intermediate	9.6±2.5	0.8±0.9	3.8±1.4	2.4±1.0
Susceptible	19.4±2.8	6.1±1.8	10.3±1.9	8.2±1.6

The mean damage values of clusters (Table 3.7b) are in agreement with Rukazambuga *et al.* (1998), who made damage groupings based on PCI. They considered 0-5% as negligible, 11-15% as moderate and 16-20% as heavy damage. Interesting to note is that all the Obino 'l Ewai derived hybrids clustered as susceptible even though their male parent Calcutta-4 was resistant. When clustering was applied to EAHBs only, most of them were grouped as intermediate (Table

3.8a and b). Note that brewing types are scattered around the clusters, with Endiirira grouping as susceptible. Cluster analysis of exotics (Table 3.9a and b) again shows that plantains are the most susceptible *Musa* subgroup. Their peripheral damage (PCI) and inner damage are also comparatively higher than the other groups.

3.3.3 Principle component analysis

Two major damage variables have been used in this study; one measuring inner damage and the other peripheral damage. Some cultivars are high in one and low in the other. For example, Nsowe and Gonja show high PCI, but low total damage. Principle component analysis was thus used to separate these variables into principle components that would give a graphical representation of cultivar response to both variables.

Table 3.10a. Correlation coefficient between four weevil damage indices. All coefficients are significant at $P<0.05$)

Damage index	1	2	3	4
1. Percentage coefficient of infestation	1.00	**0.89**	**0.94**	**0.93**
2. Total inner damage		1.00	**0.79**	**0.81**
3. PCI (Lower)			1.00	**0.96**
4. PCI (Upper)				1.00

Table 3.10b. Eigen vectors of principal components analysis using four weevil damage indices

Damage index	PC 1	PC 2
1. Percentage coefficient of infestation	**-0.51**	-0.03
2. Total inner damage	-0.47	**0.82**
3. PCI (Lower)	**-0.51**	0.43
4. PCI (Upper)	**-0.51**	0.37
Percentage of total variation:	***91.6%***	*6.4%*
Eigen Value:	***3.66***	*0.26*

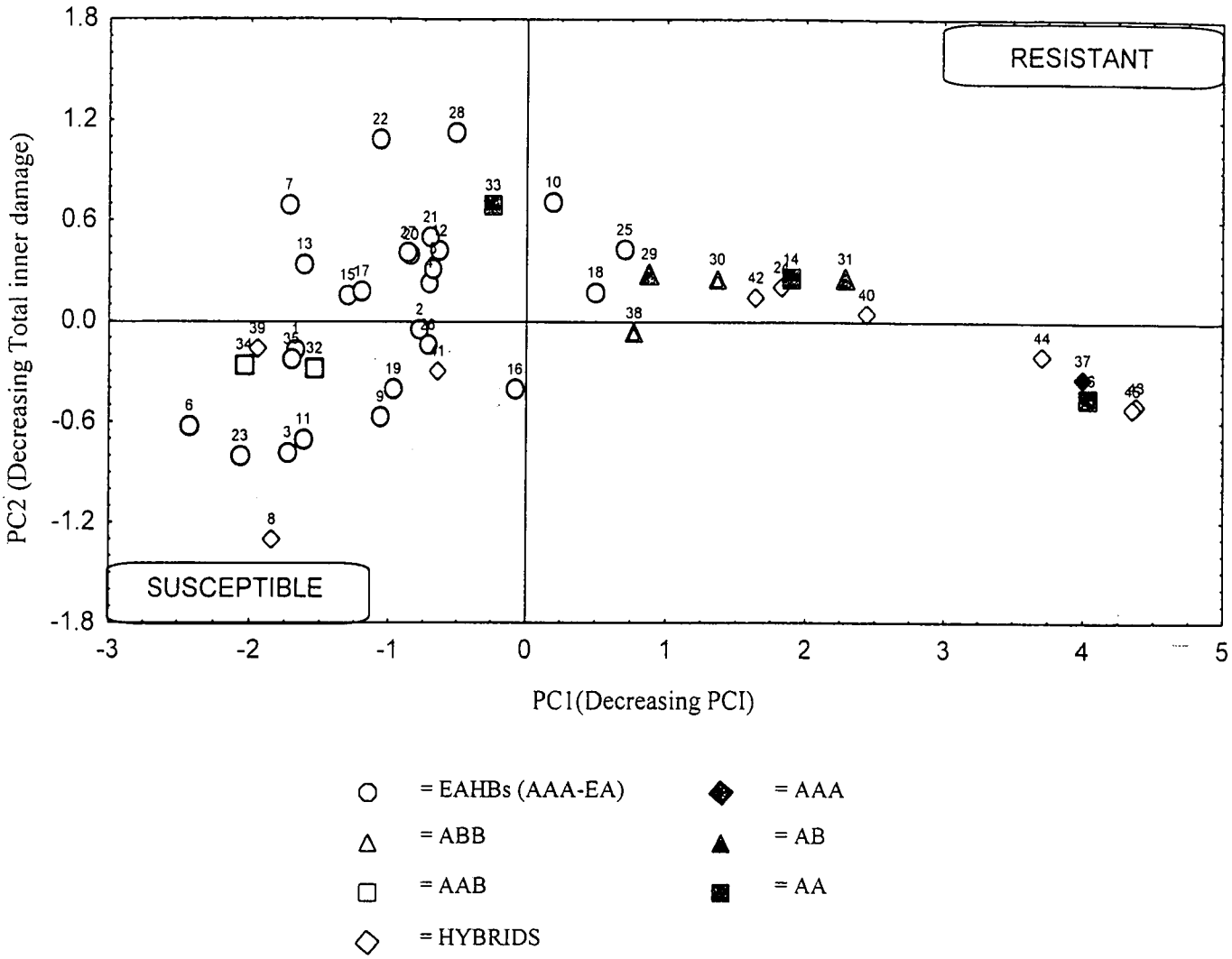
Principle component analysis based on a correlation matrix was done using total inner damage, percentage damage, and both PCI upper and PCI lower variables. These were the best variables that separated into meaningful principle components. The correlation matrix between these damage observations revealed highly significant coefficients ($P<0.005$) (Table 3.10a).

PCA reduced the four damage observations to two major components that together accounted for 98% of the original variation (Table 10b). The first and most important component, principle component one (PC1) accounted for 91.6% of the total variability in the original data. Percentage coefficient of infestation, PCI lower and PCI upper were the most important variables contributing to principal component one (PC1). Therefore PC1 was taken as a new measure for peripheral damage (taking care of PCI (upper and lower) plus percentage damage). It was then plotted with principle component two (PC2) which had a high positive correlation (0.82) with total inner damage, and contributed 6.4% of the total variation (Table 3.10b). The plot of PC1 (peripheral damage) against PC2 (total inner damage) (Figure 3.4), revealed that TMPx7152-2 was the most susceptible cultivar, with the EAHBs Ndiibwabalangira, Endirira, Nakawere and Kibuzi were also very susceptible. Most of the EAHBs, however, were intermediate, showing higher peripheral damage than inner damage (top left corner of Figure 3.4), further confirming the results from the cluster analysis.

Nalukira was the most resistant EAHB followed by Nakyetengu and Mbwazirume, all falling in the top right quarter of Figure 3.4. Overall TMB2x6142-1 and TMB2x7197-2 hybrids show the highest resistance. Kisubi, Cavendish, Kayinja, Ndiizi are the cultivars that show high resistance in terms of less peripheral and inner damage. Unfortunately they are exotic and not used for food in Uganda, but they may be included in crossing programmes to transfer resistance to more acceptable cultivars.

3.3.4 Phenotypic correlations

Correlations were performed for all data variables. This was done in the hope that phenotypic relationships between these and weevil damage would be found. First the correlations were done with all the cultivars included (Table 3.11a). Most of the banana weevil damage variables were



○ = EAHBs (AAA-EA)
◆ = AAA
△ = ABB
▲ = AB
□ = AAB
■ = AA
◇ = HYBRIDS

Key to cultivar numbers

1. Atwalira	10. Mbwazirume	19. Namwezi	28. Tereza	37. Calcutta-4
2. Bagandesza	11. Nakawere	20. Nandigobe	29. Ndiizi	38. Bluggoe
3. Endiirira	12. Bukumu	21. Mutangendo	30. Kayinja	39. TMPx5511-2
4. Enshenyi	13. Musakala	22. Nsowe	31. Kisubi	40. TMBx612-74
5. Kabula	14. Cavendish	23. Ndiibwabalangira	32. Gonja	41. TMPx7002-1
6. Kibuzi	15. Nakabululu	24. TMPx15108-6	33. Bogoya	42. FHIA03
7. Kisansa	16. Nakamali	25. Nalukira	34. Obino l'Ewai	43. TMB2x6142-1
8. TMPx7152-2	17. Nakitembe	26. Shombobuleku	35. Namafura	44. TMB2x8075-7
9. Naminwe	18. Nakyetengu	27. Siira	36. Yangambi-km5	45. TMB2x7197-2

Figure 3.4. Plot of first (PC1) and second (PC2) principle components from analysis of host plant response variables of *Musa* germplasm

significantly and strongly correlated. Considering the correlation matrix that included all the cultivars (Table 3.11a), percentage damage correlates with coefficient of infestation, percentage outer damage, and total inner damage by 0.97, 0.86 and 0.79 respectively. This implies that any one of these indices may be a sufficient measure of weevil resistance. Outer dry matter content showed a relatively high relationships between both upper and lower PCI (r=-0.50, and r=-0.48, respectively) (Table 3.11a). When EAHBs were analysed separately (Table 3.11b), percentage damage was related to inner corm hardness by r=0.41, while coefficient of infestation (visual), was related to inner corm hardness by r=45, all significant at P=0.05. This means that in EAHBs there is less damage in plants with a soft central cylinder.

Resin/sap production was found to be slightly but significantly negatively correlated to PCI upper and PCI lower at r=-0.40 and r=-0.38 respectively (Table 3.11a). It was also negatively correlated to coefficient of infestation and percentage outer damage by r=-0.33 and r=-33 respectively. These relationships although small were significant and were observed when all cultivars were analysed together (Table 3.11a).

Stronger negative relationships were found between percentage inner damage and the outer diameter (upper) of the corm (r=-0.53) within EAHB (Table 3.11b). This implies that the bigger the corm, the lesser the inner damage, therefore suggesting that corm size may be a reasonable resistance mechanism to consider in some *Musa* cultivars. Two interesting and strong relationships were observed when exotic varieties were analysed separately (Table 3.11c). Percentage damage was related to outer dry matter content by -0.59, while PCI upper and PCI lower were related to outer dry matter content by -0.68 and -0.65 respectively. All the diameters were related to outer dry matter content by greater than -0.50. Slower growing cultivars apparently also suffer less weevil damage as shown by days from flowering to harvest being negatively correlated to PCI upper and lower by r=-0.52 and r=-0.49 respectively (Table 3.11c). Percentage damage is also negatively correlated to days from flowering to harvest among exotic cultivars. This may indirectly refer to time span necessary to build dry matter content and as was seen earlier, higher dry matter contributes to resistance.

Table 3.11a. Correlation matrix for all *Musa* cultivars together (coefficients in bold font are significant at p<0.05)

		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	PCI (Upper)	**0.78**	-0.37	**0.75**	**0.36**	**0.55**	0.27	**0.55**	0.16	0.10	**0.22**	0.19	**0.69**	**0.35**	**0.62**	**0.50**	**0.43**	**-0.57**	0.00	**0.39**	0.11	**-0.44**	0.06	-0.02	0.10	**-0.50**	-0.03	**-0.40**
2	PCI (Lower)		-0.36	**0.80**	**0.39**	**0.54**	0.34	**0.63**	0.11	0.08	0.18	0.15	**0.78**	**0.42**	**0.67**	**0.56**	**0.38**	**-0.48**	-0.01	**0.31**	0.11	**-0.35**	0.08	0.01	0.16	**-0.48**	-0.04	**-0.38**
3	Suckering ability			-0.35	-0.26	-0.30	-0.23	-0.27	0.12	0.13	0.07	0.08	**-0.28**	**-0.27**	**-0.32**	-0.31	**-0.40**	**0.48**	0.13	-0.15	-0.03	**0.46**	-0.18	-0.07	-0.14	0.12	0.16	0.17
4	Percentage Damage				**0.60**	**0.70**	**0.55**	**0.81**	-0.02	-0.01	0.08	0.10	**0.97**	**0.64**	**0.86**	**0.79**	**0.35**	**-0.46**	-0.10	**0.22**	0.05	**-0.32**	0.03	-0.03	0.16	**-0.43**	-0.02	**-0.36**
5	Inner cross section (Upper)					**0.74**	**0.60**	**0.51**	**-0.25**	**-0.27**	-0.13	-0.12	**0.54**	**0.92**	**0.71**	**0.88**	**0.23**	**-0.28**	-0.28	-0.09	-0.06	**-0.28**	0.06	-0.01	0.13	-0.14	-0.02	**-0.20**
6	Outer cross section (Upper)						**0.46**	**0.53**	-0.17	-0.14	-0.01	0.02	**0.64**	**0.68**	**0.87**	**0.82**	**0.27**	**-0.36**	-0.22	0.04	-0.01	**-0.32**	0.00	-0.03	0.05	**-0.26**	-0.01	-0.27
7	Inner cross section (Lower)							**0.64**	**-0.28**	**-0.26**	-0.17	-0.16	**0.55**	**0.87**	**0.63**	**0.82**	0.14	**-0.20**	-0.18	-0.08	-0.04	-0.17	0.03	-0.02	0.08	-0.11	-0.01	-0.17
8	Outer cross section (Lower)								**-0.03**	-0.03	0.02	0.03	**0.78**	**0.64**	**0.88**	**0.79**	**0.25**	**-0.35**	-0.10	0.12	0.00	**-0.25**	-0.01	-0.02	0.16	**-0.35**	-0.03	**-0.29**
9	Inner diameter (Upper)									**0.86**	**0.74**	**0.68**	0.10	**-0.29**	-0.11	-0.23	**0.26**	**-0.26**	**0.54**	**0.58**	**0.25**	-0.06	-0.17	-0.08	-0.14	**-0.39**	0.04	-0.08
10	Outer diameter (Upper)										**0.84**	**0.85**	0.10	**-0.30**	-0.10	-0.22	0.17	-0.17	**0.63**	**0.54**	**0.29**	0.15	**-0.35**	-0.14	**-0.28**	**-0.48**	0.08	0.05
11	Inner diameter (Lower)											**0.89**	0.15	-0.16	0.01	-0.10	0.18	**-0.24**	**0.57**	**0.53**	**0.29**	0.08	**-0.26**	-0.11	**-0.23**	**-0.50**	0.07	0.04
12	Outer diameter (Lower)												0.16	-0.16	0.03	-0.08	0.13	-0.16	**0.54**	**0.46**	**0.25**	0.16	**-0.30**	-0.14	**-0.24**	**-0.50**	0.10	0.11
13	Coefficient of infestation													**0.62**	**0.83**	**0.78**	**0.26**	**-0.39**	-0.02	**0.26**	0.09	**-0.27**	-0.03	-0.05	0.17	**-0.44**	0.01	**-0.33**
14	% inner damage														**0.75**	**0.95**	**0.22**	**-0.26**	-0.26	-0.09	-0.06	**-0.26**	0.05	-0.02	0.12	-0.14	-0.02	**-0.20**
15	% outer damage															**0.92**	**0.29**	**-0.40**	-0.17	0.10	0.00	**-0.32**	0.00	-0.03	0.12	**-0.35**	-0.02	**-0.33**
16	Total inner damage																**0.27**	**-0.35**	-0.24	-0.01	-0.04	**-0.31**	0.03	-0.02	0.13	**-0.26**	-0.02	**-0.28**
17	Days to flowering																	**-0.52**	-0.05	**0.49**	0.16	**-0.60**	0.03	-0.07	0.02	**-0.30**	-0.04	-0.15
18	Days from flowering to harvest																		-0.13	**-0.41**	-0.12	**0.48**	0.09	0.10	0.02	**0.33**	0.02	**0.44**
19	Bunch weight																			**0.40**	**0.27**	**0.25**	**-0.20**	-0.11	**-0.28**	**-0.36**	0.01	-0.04
20	Plant height																				**0.30**	**-0.28**	-0.14	-0.10	-0.16	**-0.40**	0.05	**-0.23**
21	Plant girth (at 100 cm)																					-0.02	-0.11	-0.04	-0.15	-0.14	0.00	-0.09
22	Number of leaves at flowering																						-0.10	-0.02	-0.07	**0.22**	0.05	**0.25**
23	Peripheral corm hardness																							0.47	**0.62**	**0.37**	-0.09	-0.03
24	Outer corm hardness																								**0.53**	**0.22**	-0.04	-0.04
25	Inner corm hardness																									**0.29**	-0.06	-0.09
26	Outer dry matter content																										0.02	0.12
27	Inner dry matter content																											-0.03
28	Resin/sap content																											

Table 3.11b Correlation matrix for EAHB only (coefficients in bold font are significant at p<0.05)

		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	PCI (Upper)	**0.54**	-0.14	**0.57**	**0.30**	**0.40**	**0.24**	**0.43**	-0.12	-0.12	-0.07	0.01	**0.53**	**0.30**	**0.48**	0.40	0.18	-0.08	**-0.32**	-0.01	0.00	-0.15	**0.25**	**0.21**	**0.34**	-0.14	0.01	-0.13
2	PCI (Lower)		-0.17	**0.64**	**0.34**	**0.40**	**0.32**	**0.53**	-0.15	-0.13	-0.04	-0.01	**0.67**	**0.37**	**0.53**	**0.46**	0.18	-0.01	-0.26	-0.03	0.01	-0.09	0.19	**0.25**	**0.35**	**-0.21**	-0.02	-0.14
3	Suckering ability			**-0.25**	**-0.28**	**-0.35**	**-0.27**	-0.17	**0.37**	**0.34**	**0.31**	**0.26**	-0.11	**-0.30**	**-0.30**	-0.32	**-0.45**	0.19	**0.39**	0.17	0.07	**0.43**	-0.38	**-0.42**	**-0.29**	**-0.26**	-0.27	0.06
4	Percentage Damage				**0.64**	**0.66**	**0.59**	**0.78**	**-0.31**	**-0.28**	**-0.22**	-0.13	**0.97**	**0.69**	**0.82**	**0.79**	**0.20**	-0.11	**-0.40**	-0.17	-0.04	-0.14	0.19	0.16	**0.41**	-0.13	0.01	-0.17
5	Inner cross section (Upper)					**0.77**	**0.62**	**0.48**	**-0.48**	**-0.49**	**-0.29**	-0.28	**0.59**	**0.93**	**0.73**	**0.90**	**0.21**	**-0.22**	**-0.49**	**-0.32**	-0.10	**-0.21**	0.03	-0.01	0.16	-0.01	0.09	-0.11
6	Outer cross section (Upper)						**0.53**	**0.50**	**-0.46**	**-0.46**	**-0.31**	**-0.25**	**0.57**	**0.74**	**0.88**	**0.85**	**0.22**	**-0.20**	**-0.50**	**-0.28**	-0.08	**-0.30**	0.11	0.05	**0.20**	0.07	0.14	**-0.23**
7	Inner cross section (Lower)							**0.61**	**-0.49**	**-0.48**	**-0.38**	**-0.37**	**0.55**	**0.86**	**0.65**	**0.82**	0.18	-0.19	**-0.33**	**-0.29**	-0.08	-0.19	-0.03	-0.09	0.08	-0.12	-0.01	-0.11
8	Outer cross section (Lower)								**-0.27**	**-0.25**	**-0.25**	-0.19	**0.74**	**0.59**	**0.85**	**0.74**	0.17	-0.10	**-0.26**	-0.17	-0.07	-0.15	0.09	0.10	**0.29**	**-0.22**	-0.09	-0.16
9	Inner diameter (Upper)									**0.94**	**0.75**	**0.78**	-0.13	**-0.54**	**-0.42**	**-0.52**	-0.04	0.19	**0.54**	**0.61**	**0.21**	0.17	-0.12	-0.05	-0.14	**-0.37**	-0.20	0.15
10	Outer diameter (Upper)										**0.75**	**0.80**	-0.11	**-0.53**	**-0.41**	**-0.51**	-0.04	**0.21**	**0.56**	**0.63**	**0.28**	**0.20**	-0.16	-0.07	-0.17	**-0.36**	-0.19	0.09
11	Inner diameter (Lower)											**0.85**	-0.09	**-0.37**	**-0.33**	-0.37	-0.07	0.18	**0.46**	**0.55**	**0.27**	**0.26**	-0.05	0.08	-0.06	**-0.37**	-0.14	0.14
12	Outer diameter (Lower)												-0.03	**-0.35**	**-0.26**	-0.33	-0.02	0.18	**0.41**	**0.51**	**0.26**	**0.24**	-0.04	0.06	-0.01	**-0.36**	-0.15	0.06
13	Coefficient of infestation													**0.66**	**0.80**	**0.77**	0.07	-0.04	**-0.28**	-0.04	0.02	-0.09	0.14	0.16	**0.45**	-0.21	0.04	**-0.21**
14	% inner damage														**0.77**	**0.96**	**0.22**	**-0.22**	**-0.47**	**-0.35**	-0.10	**-0.23**	0.01	-0.05	0.14	-0.05	0.06	-0.12
15	% outer damage															**0.92**	**0.22**	-0.17	**-0.45**	**-0.26**	-0.09	**-0.26**	0.11	0.08	**0.28**	-0.08	0.04	**-0.22**
16	Total inner damage																**0.24**	-0.21	**-0.49**	**-0.33**	-0.10	**-0.26**	0.06	0.01	0.21	-0.07	0.05	-0.17
17	Days to flowering																	-0.09	**-0.34**	**0.17**	0.10	**-0.62**	**0.22**	0.16	0.09	0.06	0.06	**0.20**
18	Days from flowering to harvest																		**0.20**	**0.23**	0.05	0.17	-0.04	-0.16	-0.14	0.02	0.04	0.15
19	Bunch weight																			**0.40**	0.19	**0.41**	**-0.24**	**-0.23**	**-0.33**	**-0.38**	-0.27	-0.01
20	Plant height																				**0.25**	-0.10	-0.02	-0.06	**-0.22**	**-0.26**	-0.18	0.05
21	Plant girth (at 100 cm)																					0.04	-0.13	-0.06	-0.17	-0.07	0.02	-0.04
22	Number of leaves at flowering																						-0.14	-0.09	-0.07	-0.10	-0.05	-0.15
23	Peripheral corm hardness																							**0.62**	**0.58**	0.16	0.26	0.08
24	Outer corm hardness																								**0.69**	0.12	0.22	0.02
25	Inner corm hardness																									0.08	0.17	0.04
26	Outer dry matter content																										**0.60**	0.14
27	Inner dry matter content																											-0.01
28	Resin/sap content																											

Table 3.11c. Correlation matrix for exotic *Musa* cultivars only (coefficients in bold font are significant at p<0.05)

		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	PCI (Upper)	**0.86**	**-0.21**	**0.85**	**0.43**	**0.72**	**0.29**	**0.61**	**0.27**	**0.39**	**0.50**	**0.51**	**0.80**	**0.38**	**0.75**	**0.61**	**0.38**	**-0.52**	0.14	**0.47**	**0.38**	**-0.30**	**-0.31**	**-0.21**	**-0.30**	**-0.68**	0.01	**-0.20**
2	PCI (Lower)		**-0.23**	**0.90**	**0.46**	**0.70**	**0.36**	**0.68**	**0.24**	**0.36**	**0.43**	**0.44**	**0.86**	**0.45**	**0.79**	**0.66**	**0.34**	**-0.49**	0.15	**0.41**	**0.39**	**-0.24**	**-0.23**	**-0.21**	**-0.24**	**-0.65**	-0.01	**-0.24**
3	Suckering ability			**-0.25**	-0.14	-0.17	-0.18	-0.23	0.09	-0.06	-0.09	-0.13	**-0.23**	-0.18	**-0.23**	**-0.22**	**-0.23**	**0.29**	0.05	-0.12	-0.11	0.19	0.12	0.13	0.17	0.21	0.17	-0.16
4	Percentage Damage				**0.54**	**0.74**	**0.51**	**0.82**	0.15	**0.28**	**0.37**	**0.40**	**0.97**	**0.58**	**0.89**	**0.79**	**0.31**	**-0.50**	0.09	**0.38**	**0.32**	**-0.24**	**-0.28**	-0.19	**-0.24**	**-0.59**	0.01	**-0.27**
5	Inner cross section (Upper)					**0.64**	**0.63**	**0.63**	-0.04	0.01	0.16	0.16	**0.39**	**0.87**	**0.72**	**0.86**	0.16	**-0.28**	-0.03	0.12	0.08	**-0.20**	-0.04	-0.07	-0.04	**-0.25**	-0.02	-0.19
6	Outer cross section (Upper)						**0.31**	**0.54**	0.07	0.18	**0.33**	**0.36**	**0.69**	**0.49**	**0.85**	**0.72**	**0.24**	**-0.47**	0.06	**0.28**	**0.24**	**-0.25**	**-0.27**	-0.16	**-0.31**	**-0.48**	0.00	-0.18
7	Inner cross section (Lower)							**0.68**	-0.13	-0.10	0.01	0.01	**0.55**	**0.93**	**0.58**	**0.82**	0.05	**-0.21**	-0.01	0.12	0.07	-0.06	0.06	0.02	0.06	-0.11	-0.01	**-0.25**
8	Outer cross section (Lower)								0.12	**0.20**	**0.28**	**0.28**	**0.84**	**0.73**	**0.90**	**0.88**	**0.21**	**-0.41**	0.04	**0.27**	**0.21**	**-0.20**	-0.19	-0.12	-0.07	**-0.41**	-0.02	**-0.28**
9	Inner diameter (Upper)									**0.88**	**0.77**	**0.70**	0.19	-0.10	0.11	0.00	**0.37**	**-0.35**	**0.55**	**0.57**	**0.68**	-0.08	**-0.24**	-0.10	-0.18	**-0.40**	0.06	-0.19
10	Outer diameter (Upper)										**0.88**	**0.85**	**0.30**	-0.06	**0.22**	0.08	**0.38**	**-0.49**	**0.70**	**0.65**	**0.83**	-0.01	**-0.40**	-0.15	**-0.31**	**-0.56**	0.08	-0.18
11	Inner diameter (Lower)											**0.91**	**0.37**	0.08	**0.34**	0.23	**0.35**	**-0.50**	**0.64**	**0.60**	**0.76**	-0.07	**-0.35**	-0.18	**-0.34**	**-0.57**	0.07	-0.15
12	Outer diameter (Lower)												**0.40**	0.08	**0.36**	**0.24**	**0.32**	**-0.50**	**0.64**	**0.59**	**0.74**	-0.04	**-0.37**	-0.19	**-0.33**	**-0.58**	0.10	-0.07
13	Coefficient of infestation													**0.55**	**0.83**	**0.77**	**0.23**	**-0.41**	0.12	**0.33**	**0.32**	-0.19	**-0.26**	-0.18	**-0.21**	**-0.58**	0.07	-0.18
14	% inner damage														**0.71**	**0.93**	0.12	**-0.27**	-0.03	0.13	0.09	-0.14	0.02	-0.02	0.02	-0.19	-0.02	**-0.25**
15	% outer damage															**0.92**	**0.25**	**-0.49**	0.06	**0.31**	**0.26**	**-0.25**	**-0.26**	-0.16	**-0.21**	**-0.50**	-0.01	**-0.28**
16	Total inner damage																**0.21**	**-0.43**	0.02	**0.25**	**0.20**	**-0.22**	-0.12	-0.09	-0.10	-0.37	-0.02	**-0.28**
17	Days to flowering																	**-0.53**	0.08	**0.58**	**0.38**	-0.15	-0.16	-0.18	-0.14	-0.40	-0.02	-0.02
18	Days from flowering to harvest																		**-0.23**	**-0.49**	**-0.46**	**0.26**	**0.36**	**0.22**	**0.31**	0.42	-0.05	**0.20**
19	Bunch weight																			**0.41**	**0.79**	**0.29**	-0.18	-0.04	**-0.24**	-0.37	0.03	-0.08
20	Plant height																				**0.71**	-0.17	**-0.34**	-0.15	**-0.21**	-0.47	0.11	-0.17
21	Plant girth (at 100 cm)																					0.10	**-0.34**	-0.09	**-0.29**	**-0.56**	0.04	-0.15
22	Number of leaves at flowering																						0.14	0.06	0.14	**0.33**	-0.01	0.03
23	Peripheral corm hardness																							**0.37**	**0.62**	**0.55**	-0.11	0.18
24	Outer corm hardness																								**0.44**	**0.26**	-0.05	0.04
25	Inner corm hardness																									**0.50**	-0.08	-0.03
26	Outer dry matter content																										-0.01	0.08
27	Inner dry matter content																											-0.14
28	Resin/sap content																											

3.3.5 Clonal heritabilities and genetic correlations

Estimates of heritabilities, genetic variances as well as means, F and P values of the ANOVAs for each of the variables are given in Table 3.12. Broad sense estimates of clonal heritabilities were quite variable, ranging from 0.05 for outer hardness to 0.99 for plant girth. The genetic variances indicate the genetic variability of the population, while the heritabilities reflect the extent of genetic control and potential advance that may be made for each character during a selection programme (Hanson, 1963). In Table 3.12 it is evident that the characters measured are quite variable and generally highly heritable. Total inner damage would in this case be the best character for selecting for weevil resistance, because it scores the highest heritability estimate of all the weevil damage indices.

The cultivars exhibited strong genetic variances for some key measured variables and traits. Plant girth at 100 cm above the ground level had the highest (0.99) broad sense heritability among clones of *Musa* germplasm in Uganda. Some workers (Bosch *et al.*, 1995) on banana agronomy have found a high and significantly positive relationship between this trait and yield in terms of bunch weight.

Heritability estimates measure the efficiency of a selection programme, based on that character. Thus it indicates how much variation in the character is genetically controlled. The use of clonal material obviously increases the size of heritability values but they are nevertheless comparatively important (Burton and DeVane, 1953). Also, since the crop is vegetatively propagated, the values of heritability are appropriate for selection, even if they are overestimated due to dominance and epistatic effects (Keller and Likens, 1955).

Total inner damage was the banana weevil related trait that showed the highest heritability (0.87). This same trait was used in the previous sections as a basis for ranking the response of cultivars to banana weevil damage. This trait can therefore be solely used for the successful selection of banana weevil resistance. Estimated genetic correlations for all the variables measured are given in Table 3.13. Correlations with outer hardness could not be calculated due to a negative estimate of genetic variance (Mitchell and Shaw, 1993) and as observed in the matrix, some coefficients are greater than unity. This is expected of estimated correlation coefficients (Baker, 1986; Rowe and Brink, 1993). Several genetic correlations are larger

Table 3.12. Estimates of clonal heritabilities and genetic variances for different traits in *Musa* (* = ANOVA not significant)

Variable	Heritability	Mean	Variance	F	P Value
Plant girth (at 100 cm)	0.99	446.02	1793.55	356.35	0.0001
Total inner damage	0.87	3.57	7.05	3.20	0.0001
Days from flowering to harvest	0.60	134.86	1079.82	5.56	0.0001
Outer corm diameter (upper)	0.58	15.65	3.61	5.23	0.0001
Number of functional leaves at flowering	0.57	8.43	4.89	5.04	0.0001
PCI Upper	0.55	6.72	6.86	4.75	0.0001
Plant height	0.55	254.66	890.46	4.72	0.0001
Resin/Sap content	0.53	2.90	2.52	4.49	0.0001
Percentage peripheral damage	0.52	11.56	25.13	4.27	0.0001
Suckering ability	0.48	7.30	6.63	3.81	0.0001
PCI Lower	0.47	5.77	5.92	3.69	0.0001
Inner diameter (Lower)	0.47	11.21	1.51	3.67	0.0001
Outer diameter (Lower)	0.44	15.32	3.79	2.84	0.0001
Peripheral hardness	0.43	178.59	337.38	3.30	0.0001
Days from planting to flowering	0.43	416.83	1499.35	3.30	0.0001
Bunch weight	0.41	9.14	7.91	3.15	0.0001
Coefficient of infestation (visual)	0.41	9.29	18.46	3.11	0.0001
Percentage Cross section damage outer	0.40	5.08	6.87	3.05	0.0001
Percentage cross section damage inner	0.36	2.05	4.09	2.72	0.0001
Inner cross section damage (Upper)	0.35	2.64	6.83	2.62	0.0001
Inner cross section damage (Lower)	0.34	1.46	3.57	2.57	0.0001
Outer cross section damage (Outer)	0.29	4.65	5.83	2.28	0.0007
Outer cross section damage (Lower)	0.29	5.51	7.26	2.26	0.0008
Inner dry matter content	0.27	0.14	0.06	2.14	0.001
Outer dry matter content	0.20	0.13	0.00	5.08	0.0001
Inner diameter (upper)*	0.19	10.73	0.55	1.69	0.2100
Inner hardness*	0.08	144.79	68.57	1.27	0.1700
Outer hardness*	0.05	174.31	-47.23	0.86	0.6900

than the phenotypic correlations calculated in section 3.3.4 (Table 3.11a). This is also expected, since at genetic level more strict relationships are expected and the implication here is that there is significant environmental influence in the expression of traits. Based on genetic correlations, the most important structural factors that are highly related to banana weevil resistance, are peripheral and inner corm hardness plus resin/sap production. Taking total inner damage as an example, its negative correlation with peripheral and inner corm hardness is close to unity. These variables did not show strong phenotypic correlations when all cultivars were analysed together in Table 3.11a. Outer diameter (lower), which translates to corm size, may also be an important resistance mechanism, since it correlates positively with total inner damage at r=0.62. Days from flowering to harvest, shows a strong relationship with damage and may be an indirect indicator of resistance. Apart from damage indices there was little correspondence between the genetic and phenotypic correlation matrices. All the banana weevil damage variables were strongly genetically correlated with each other, indicating that such associations are due to a common genetic background. High negative correlations were found between peripheral corm hardness, inner corm hardness and resin content with total inner damage. Such correlations are important because they may be the mechanisms of banana weevil resistance in *Musa*. The phenotypic and genetic correlations given are important in a selection programme intended to increase the resistance to banana weevil. Other traits like bunch weight, show a positive genetic correlation with peripheral and outer damage, implying that cultivars with large bunch weights may be susceptible to banana weevil. This perhaps best illustrates the need for genetic correlation estimates. These relationships need to remain in the mind of a breeder for better and successful selections. Selecting only one character, for example, would result in progress for all positively correlated characters and regress of all negatively correlated characters.

3.5 Discussion

Banana weevil has until recently not been considered an important pest, mainly because the large commercial farms in South America and the Caribbean can effectively control the pest using chemicals. However, banana weevil is reported to be an important pest, which reduces yields in tropical areas, where banana is a very important subsistence staple.

Table 3.13 Genetic correlation coefficients between all measured variables. Some estimated genetic correlations have absolute values greater than 1, indicating that the true correlations are near 1 or –1. Some genetic correlations could not be estimated (significance was not tested)

		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	PCI (Upper)	1.72	2.04	1.22	1.48	0.74	1.70	0.44	0.53	0.64	0.75	1.90	1.05	1.57	-1.23	1.24	1.50	-2.16	0.80	1.96	0.41	-1.36	-1.27	-	-1.47	-0.03	0.07	-0.86
2	PCI (Lower)		2.20	1.08	1.37	0.66	1.70	0.43	0.39	0.50	0.55	2.00	0.92	1.52	-1.61	1.17	1.78	-2.62	0.69	2.06	0.41	-1.50	-1.18	-	-0.91	-0.03	0.04	-0.98
3	Percentage Damage			1.51	1.98	1.21	2.26	0.40	0.60	0.74	0.96	3.20	1.39	2.11	-1.47	1.72	2.47	-4.19	0.88	3.52	0.75	-1.49	-3.01	-	-2.89	-0.03	0.08	-1.05
4	Inner cross section (Upper)				1.38	0.92	1.71	-0.10	-0.07	0.15	0.26	1.58	1.48	1.53	-0.59	1.42	0.32	-0.96	0.28	0.92	-0.19	-0.55	-0.24	-	-0.97	-0.02	0.03	-0.69
5	Outer cross section (Upper)					1.00	1.99	0.32	0.68	0.79	1.13	1.95	1.26	1.83	-0.70	1.46	0.17	-1.59	1.06	1.35	0.21	-0.45	-1.76	-	-2.94	-0.03	0.13	-0.88
6	Inner cross section (Lower)						1.37	0.07	0.11	0.43	0.54	1.33	1.18	1.17	-0.05	1.08	-0.23	-0.44	0.01	0.48	-0.06	-0.35	-0.88	-	-1.21	-0.01	0.22	-0.50
7	Outer cross section (Lower)							0.26	0.34	0.61	0.73	2.17	1.62	1.92	-1.17	1.68	1.15	-2.33	0.59	1.72	0.03	-1.32	-1.91	-	-2.04	-0.03	0.12	-1.13
8	Inner diameter (Upper)								0.67	0.67	0.61	0.30	-0.03	0.28	-0.48	0.13	0.74	-0.71	0.70	0.59	0.24	-0.28	-0.33	-	-0.31	-0.02	0.00	-0.16
9	Outer diameter (Upper)									1.02	1.34	0.52	0.01	0.50	-0.25	0.25	0.96	-0.65	1.23	0.67	0.56	0.01	-1.14	-	-1.31	-0.03	0.03	0.18
10	Inner diameter (Lower)										1.05	0.71	0.30	0.68	-0.27	0.46	0.51	-0.56	0.81	0.50	0.39	-0.07	-0.67	-	-0.47	-0.03	0.03	0.07
11	Outer diameter (Lower)											0.93	0.41	0.91	-0.18	0.62	0.50	-0.62	1.26	0.59	0.56	0.09	-1.12	-	-0.93	-0.03	0.04	0.15
12	Coefficient of infestation												1.50	2.05	-1.42	1.73	1.81	-3.16	0.79	2.70	0.59	-1.34	-2.47	-	-2.31	-0.02	-0.02	-1.02
13	% inner damage													1.43	-0.36	1.32	0.05	-0.70	0.16	0.70	-0.13	-0.48	-0.56	-	-1.10	-0.02	0.12	-0.65
14	% outer damage														-0.93	1.55	0.66	-1.96	0.81	1.53	0.12	-0.88	-1.84	-	-2.48	-0.03	0.12	-0.99
15	Suckering ability															-0.62	-1.60	2.01	-0.46	-1.80	-0.31	1.50	0.86	-	1.10	0.02	0.05	0.75
16	Total inner damage																0.35	-1.33	0.47	1.12	0.00	-0.65	-1.20	-	-1.78	-0.02	0.11	-0.76
17	Days to flowering																	-1.10	1.60		8.50	-1.75	-2.92	-	-2.03	-0.02	0.02	-0.49
18	Days from flowering to harvest																		-1.13		-3.75	1.98	3.12	-	2.05	0.02	-0.02	1.00
19	Bunch weight																			0.54	0.74	-0.21	-0.46	-	-1.11	-0.03	-0.04	0.09
20	Plant height																				7.09	-1.46	-4.62	-	-1.95	-0.02	0.04	-0.89
21	Plant girth (at 100 cm)																					-0.11	-2.94	-	-4.80	0.00	0.00	-0.22
22	Number of leaves at flowering																						0.16	-	0.17	0.02	0.02	0.76
23	Peripheral corm hardness																							-	5.82	0.02	-0.09	0.20
24	Outer corm hardness																								3.37	-	-	-
25	Inner corm hardness																									0.03	-0.06	0.54
26	Outer dry matter content																										-0.01	0.01
27	Inner dry matter content																											0.01
28	Resin/sap content																											

This study has revealed a wide range of host plant responses to banana weevil. Between genome groups it has been observed that plantains suffer the highest damage followed by EAHBs. These are important food crops in West and East Africa respectively. Even hybrids of plantains have shown high levels of banana weevil damage. Plantains, as the most susceptible genome group, have already been reported from several other studies (Ittyepe, 1986; Speijer *et al.*, 1993; Seshu-Reddy and Lubega, 1993; Fogain and Price, 1994; Gold *et al.*, 1994b; Ortiz *et al.*, 1995). It is interesting to note that Mbwazirume and Nakyetengu, two of the most important cooking cultivars in Uganda, are relatively resistant. They are well-distributed throughout the banana growing regions of Uganda and farmers report high preference for them (Gold *et al.*, 1997a). Some other reasons why these two lines are popular are that they give big bunch weights (=higher yield), show resistance to stress and have a good taste. Nakyetengu in particular is a stout variety making it resistant to wind damage. Speijer *et al.* (1998) evaluated host plant response to nematodes and have reported Mbwazirume as more resistant to nematodes compared to other EAHB cultivars.

Some EAHBs have consistently shown moderate resistance levels in this study. Comparisons of weevil damage scores to site means (Z scores), from the Uganda nation-wide diagnostic survey (Gold *et al.*, 1993), suggested a wide range of variability, but with most of the cultivars showing average susceptibility. This moderate resistance may be due to antibiosis, as several workers have already indicated (Pavis and Minost, 1993; Ortiz *et al.*, 1995; Abera, 1998). If this is true, probably even with some of the present cultivars, an effective IPM strategy can be devised that could go a long way in controlling banana weevil. The use of resistant cultivars in IPM acts by reducing the rate of weevil population build up and this could be effectively achieved with moderate levels of host resistance, especially if it is antibiotic in nature (de Ponti, 1982; Pathak, 1991). Together with other cultural control measures like removal of post harvest residues and trapping, it should be possible to keep banana plantations free of destructive levels of banana weevil. Gold *et al.* (1997b) have reported that moderate to intensive sanitation significantly lowered both weevil population numbers and damage levels due to banana weevil.

Several resistance mechanisms or factors could be inferred from this study. Although corm hardness was considered by several workers (Ortiz *et al.*, 1995; Pavis and Lemaire, 1997) as a resistance mechanism, this study did not find a phenotypic relationship between corm hardness and weevil damage. However, genetic relationships between corm hardness and

weevil damage were sufficiently high and significant. Problems were experienced during measurement of this variable because a banana corm is not equally hard all over due to root vesicles criss-crossing the cortex, thus affecting the uniformity of data for this variable. Dry matter content in the outer cortex seems to be an important factor against banana weevil development and an indirect and better measure of tissue hardness, while corm size may be assisting in reducing weevil access to the more delicate inner tissues. According to observations on weevil development, weevil larvae, while burrowing into the corm, at a certain stage turn and start burrowing towards the outside. Thus if the corm is big this turn is made well before the central cylinder is reached, therefore avoiding its damage. Resin/sap production may also have an influence on the development and survival of banana weevil eggs and/or larvae. The exact mechanism here requires further study.

The wild diploid banana Calcutta-4 and cultivars Yangambi-km5 and FHIA-03 showed high levels of resistance to banana weevil and may be exploited as sources of resistance genes. Calcutta-4 has also been reported to be resistant to leaf decreases and has been successfully used in conventional breeding in Nigeria and Uganda (Ortiz *et al.*, 1995; Hartman *et al.*, 1999). Yangambi-km5 was recently found to be resistant to banana weevil (Lemaire, 1996). The male/female fertility of Yangambi-km5 and FHIA-03 need to be investigated so that they can be used in breeding for banana weevil resistance through conventional crossing.

This study has greatly added to knowledge of the genetic control of banana weevil resistance variables and to some extent other agronomic and plant growth related traits. Until now, no heritability estimates or genetic correlation determination of banana weevil damage traits have been attempted in *Musa*. Results indicated that *Musa* germplasm in Uganda contains a high reservoir of genetic variance for banana weevil resistance plus other growth parameters. Total inner damage seems to be the most important selection traits for banana weevil damage resistance and besides PCI, it is the first time this trait has been used. Since it correlated with bunch weight by a significant $r=0.47$, selecting for low values of total inner damage may lead to lower bunch weights and this is not desirable to farmers. One survey study revealed that bunch size was one of the most important farmer selection criteria (Gold *et al.*, 1998). The same is true for other traits, such as days to flowering and harvest (earliness), since these translate to better food security throughout the year for the mainly subsistence farmers.

CHAPTER IV

COMPONENTS OF RESISTANCE TO BANANA WEEVIL (*COSMOPOLITES SORDIDUS*) IN *MUSA* GERMPLASM IN UGANDA

4.1 Introduction

Banana weevil is a very important pest in subsistence banana and plantain cropping systems. It has been reported to cause yield and crop losses of up to 100%, thus threatening food security and livelihood in small mostly African and Asian homesteads. Host plant resistance is considered to be the most effective means of controlling the banana weevil. Some progress has been achieved in screening host plants for resistance, and some cultivars have been identified as possible sources of resistance. An understanding of the resistance mechanisms remains unclear.

Antixenosis is usually the first line of defense a pest has to face before making use of a host plant. Insects encounter volatiles, surface waxes, and ovipositional deterrents of the host plant before they can feed or oviposit (Panda and Khush, 1995). Buddenburg *et al.* (1993) identified banana kairomones as important in attracting banana weevils to their host plants. These are mostly emitted by freshly cut pseudostems and this phenomenon is useful in trapping banana weevils for population control. Several workers have attempted to determine banana weevil attraction and preference to different cultivars for feeding and/or oviposition, and here we find a rather consistent pattern. Pavis and Minost (1993) and Musabyimana (1995) did not find any correlation between attractivity and weevil infestation, with susceptible cultivars being as attractive as resistant ones. Abera (1998) found even more oviposition on some resistant cultivars than susceptible ones. These studies seem to indicate that non-preference or antixenosis is not likely an important component of weevil resistance in *Musa*.

Studies on weevil attraction to different varieties of host plants have pointed towards antibiosis as the most likely resistance mechanism in banana, and indeed studies are beginning to show that there is a differential effect of cultivar on the development and survival of banana weevil. Rukazambuga (1996) has reported slow rates of weevil population build-up and this coupled with a large discrepancy between egg and immature stage numbers

(Abera *et al.*, 1997), suggests a high mortality of eggs and early larval stages. This however may be more so on certain cultivars than others (Gold *et al.*, 1999c). Abera *et al.* (1997) found 6-12 times (depending on cultivar) more eggs than immature stages from dissected banana plants. The question arising from this is what happens to the majority of the eggs? While Lemaire (1996) found differences in developmental rates and effects on survival of banana larvae, due to cultivar differences. Banana weevils lay eggs in cavities made by the female's rostrum in the lower pseudostem or upper corm (leaf sheath) areas. On hatching the larvae burrow into the corm tissue as they develop and the feeding tunnels become longer and wider as the larvae grow. The larvae eventually complete their development while inside the plant tissue. It has been observed that the extent of tunneling depends on the number of larvae, the cultivar and plant vigour. This mode of development (inside the corm) exposes the postembryonic weevil stages to plant biotic defense mechanisms, such as tissue hardness and toxic secondary metabolic substances, which may kill off a significant number of the immature stages.

The objectives of this study, therefore, were to investigate mechanisms of banana weevil resistance, within a representative sample of *Musa* germplasm in Uganda. The main focus was to find more information on antibiosis than that suggested by various studies cited above and in Chapter II.

4.2 Materials and methods

All the weevils used in these experiments were collected from farmer's fields and maintained in the laboratory in 2-3 liter plastic containers, where they were regularly provided with fresh banana corm material for feeding. Cleaning was also done regularly, by washing the containers to remove rotting food material. Due to difficulties in obtaining sufficiently good quality plant material, there are differences in the number and cultivars used in the various experiments. The experiments were carried out at Kawanda Agricultural Research Institute (KARI), Kawanda, Uganda, which is located about 13 km north of Kampala. The mean annual temperature and relative humidity of the laboratory was 20-27°C and 76.3% respectively. The plant materials were collected from the National Banana Research Program

germplasm collection at KARI. This collection is well maintained by application of manure and mulching and insecticides are used to control pests.

4.2.1 Antixenosis

Three types of experiments were used to study antixenotic resistance. Trapping was done at the base of each plant in the field experiment, of which the design was described in Chapter III. This was followed by choice and no-choice experiments in the laboratory (see section 4.2.1.2).

4.2.1.1 Field trial trapping

Trapping weevils was carried out at three times, in January, July and October 1998. Banana weevils are known to be attracted to freshly cut banana pseudostems (Budenberg *et al.*, 1993) and this attractiveness has been used to try to control weevil populations (Bakyalire and Ogenga-Latigo, 1993). Trapping was done by using split pseudostem traps of susceptible check cultivar Atwalira, made from 30-40 cm pieces of fresh pseudostem cut in

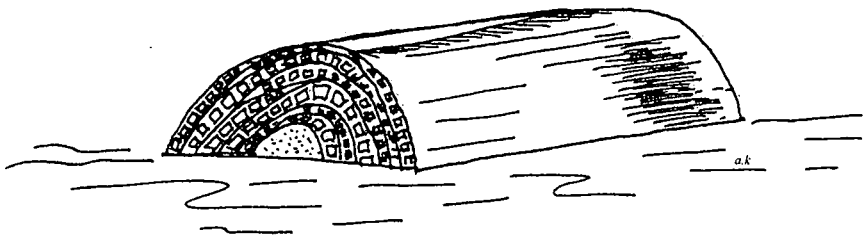


Figure 4.1. Split pseudostem trap

half lengthwise (Figure 4.1). The two halves were placed on either side of the banana plant with the flat side facing the soil, and were removed after three days and the number of marked and unmarked weevils recorded (weevil marking is described in Chapter III, section 3.2.3).

4.2.1.2 Choice experiments

Four pieces of equal sized corm and pseudostem from four different cultivars were placed at equal distances from one another in 10-liter plastic basins of which the bottoms were covered with clean moistened sand. Fifty female weevils were released in the center of the basins and the basins covered with black polythene sheets perforated with holes to provide adequate ventilation (Figure 4.2). The arrangement was left for 24 hours, after which the number of

adults found on and around each piece was counted. The corm pieces were then dissected by peeling off thin layers of tissue to reveal oviposited eggs, which were also counted. The experiment was repeated for 30 random combinations of 16 cultivars in groups of four and replicated five times. The data was pooled for analysis.

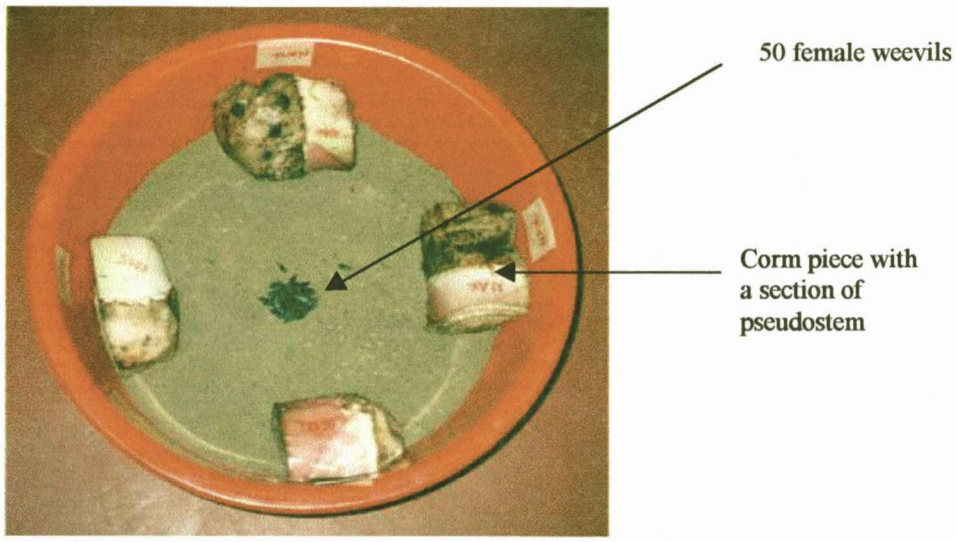


Figure 4.2. Arrangement of corm pieces of four different *Musa* cultivars in a choice experiment

4.2.1.3 No choice experiments

In the no choice experiments, equal sized pieces of corm material from 16 different cultivars were placed in individual 500 ml plastic containers, the sides of which were perforated to provide adequate ventilation. Ten female weevils were released into each container and left covered for 24 hours. The corm pieces were then removed and, dissected by peeling off thin layers of tissue to expose eggs, which were counted. The experiment was repeated 10 times with a different set of weevils, and data pooled for analysis.

4.2.2 Antibiosis

Antibiosis experiments were designed to investigate the biological effect of different corm material on the development of banana weevil eggs and larvae. All together four different experiments were carried out, *i.e.* developmental bioassays up to larval stage and another up to pupal stage, immature stages from continuous development in relatively fresh material and an egg hatchability bioassay. In these experiments the banana weevil eggs used, were

obtained by inducing adult female weevils to oviposit on big, freshly collected corms, containing 30 cm of lower pseudostem. Previous studies and experience has shown that weevils preferred to oviposit at the collar region (Abera, 1998). The corm and pseudostem pieces (2-3) were each placed in a 10-liter plastic bucket, after which approximately 100 female weevils were released into each bucket. The buckets were left covered for 24 hours after which thin layers of tissue were slowly removed to expose the eggs. These were collected and washed in a petri dish containing a 40% solution of ethanol. The eggs were then arranged on moist pieces of tissue paper in clean plastic petri dishes, previously washed in detergent, rinsed and disinfected by spraying with 75% ethanol. The petri dishes were placed in a cool place and eggs allowed to incubate at room temperature. Incubation lasted about 5-6 days.

4.2.2.1 Experiment 1 - Post-embryonic developmental to larvae up to 15 days

With the help of a fine camel hair brush, first instar larvae incubated in the laboratory were each placed on a small piece of corm tissue (5 cm x 5 cm x 1 cm) from each of the test cultivars, using medium sized pre-flowered plants. A small hole was made into the corm piece to simulate a gallery thus making it easier for the small larvae to start burrowing. Although the replications for each cultivar depended on the number of eggs collected that day, care was taken to ensure that all the test cultivars were included during each replication. The corm pieces were changed after two weeks and data taken on the number of larvae surviving. The date of first instar release onto the corm tissue varied by at least one day, since eggs hatched over a two-day period. The experiment was terminated after a period of 15 days, when larvae were expected to be in the 4th instar (Gold *et al.*, 1999a). From methods developed by Gold *et al.* (1999a), head capsule widths of larvae were determined by measuring the dorsal inter-ocular plane using a binocular dissecting microscope fitted with a calibrated micrometer eyepiece, at a magnification of x40. Each division on the micrometer was 0.0239 mm, but data was analysed in microscopic units. Data on mortality and larval weights were also taken. Using results and suggestions on instar duration by Gold *et al.* (1999a), instar stages were estimated from head capsule size. The experiment was repeated until each cultivar had 60 larvae (60 replications).

4.2.2.2 Experiment 2 -Postembryonic development up to pupal stage

This experiment was similar to experiment I, with the exception that here replications were increased to 100 and the experiment extended up to pupation. Data on mortality, days to pupation, and pupal weights were obtained. Larvae were weighted using a digital analytical balance (Mettler AE50, Precision ±0.0001 and Max. Load 50.g).

4.2.2.3 Experiment 3 - Post embryonic development in intact corms of different cultivars

In this experiment corms from different cultivars with 30-cm pieces of pseudostem were placed in 20-liter plastic buckets with sterilised sawdust at the bottom. Fifty female weevils were released into each bucket for a period of 24 hours, and then removed. Inspection was made on the corms to ensure that the weevils had sufficiently oviposited on each of them. The corm pieces were watered regularly to keep them fresh and to encourage them to sprout and root (*i.e.* to remain as fresh as possible). After 27 days when the larvae were expected to be at pupal stage, the corms were removed, dissected and the number of all the immatures recorded. The experiment was replicated three times.

4.2.2.4 Experiment 4 - Effect of sap on egg hatchability

To study the effect of sap on the hatchability of banana weevil eggs, sap was collected from maiden plants of different cultivars growing in the germplasm collection at KARI. To collect the sap a diagonal cut was made across an exposed collar region, and the exuding sap allowed to drip into small glass vials. The sap was immediately taken to the lab and dabbed onto incubating eggs in petri dishes as described in experiment I above. At the end of incubation (six days) observations on egg hatchability and condition of hatched larvae were made.

4.2.3 Data analysis

Data from the field trapping studies were analysed using general linear models of analysis of variance and that from all the laboratory experiments was analysed using one way analysis of variance (ANOVA). Means were separated using least significant difference (LSD), at the 5% probability level.

Table 4.1. Mean trap catches of banana weevils in the screening trial. Means followed by the same letter are not significantly different at P>0.05 (ANOVA F=1.37; P=0.06)

Name	Mean trap catch
Obino l'Ewai	5.55 a
Nandigobe	4.55 ab
TMB2x7197-2	4.10 abc
FHIA03	4.10 abcd
TMPx7152-2	4.06 abcde
TMPx15108-6	3.85 abcdef
TMP2x6142-1	3.70 bcdefg
TMPx5511-2	3.50 bcdefgh
Yangambi KM5	3.45 bcdefgh
TMPx7002-1	3.45 bcdefgh
Nsowe	3.40 bcdefghi
Gonja	3.35 bcdefghi
Endiirira	3.33 bcdefghi
Mutangendo	3.20 bcdefghi
Naminwe	3.05 bcdefghi
Kibuzi	2.94 bcdefghi
Musakala	2.85 bcdefghi
Bluggoe	2.80 bcdefghi
Kabula	2.75 bcdefghi
Kayinja	2.75 bcdefghi
Nakitembe	2.75 bcdefghi
Tereza	2.70 cdefghi
TMBx612-74	2.70 cdefghi
TMB2x8075-7	2.65 cdefghi
Nakabululu	2.65 cdefghi
Cavendish	2.60 cdefghi
Mbwazirume	2.60 cdefghi
Siira	2.60 cdefghi
Shombobureku	2.55 cdefghi
Nakamali	2.50 cdefghi
Ndiizi	2.50 cdefghi
Kisansa	2.44 cdefghi
Bukumu	2.40 cdefghi
Calcutta-4	2.35 cdefghi
Nakyetengu	2.33 cdefghi
Bogoya	2.20 defghi
Namwezi	2.20 defghi
Ndiibwabalangira	2.20 defghi
Bagandeseza	2.11 defghi
Nalukira	2.10 efghi
Namafura	2.05 fghi
Nakawere	2.00 fghi
Enshenyi	1.90 ghi
Kisubi	1.80 hi
Atwalira	1.60 i

4.3 Results

4.3.1 Antibiosis

Trap catches ranged from 1.60 to 5.5 weevils per cultivar. The differences in number of weevils trapped at the base of different cultivars as an indication of plant attraction were barely significant (Table 1). The means and rankings did not reflect the known cultivar responses to weevil damage. For example, although Obino l'Ewai is known to be very susceptible and ranks first in attractiveness, it was not significantly different from other resistant clones like TMB2x7197-2, FHIA03 and TMP15108-6 (see Table 3.3, Chapter III for resistance response). There were no significant differences when number of marked weevils, number of unmarked weevils and cumulative trap catches were analysed. Summarised ANOVAs for these parameters are presented in Table 4.2.

From laboratory no-choice experiments there were three groups of cultivars showing slight differences in ovipositional preference although the ANOVA was not significant (Table 4.3). Gonja was more preferred for oviposition but this response was not significantly different from other cultivers up to FHIA-03 in Table 4.3. FHIA-03, Atwalira, Nakyetengu, and Muvubo showed higher preference than Gonja. Note that even Yangambi-km5, a well-known resistant variety, attracted the same amount of oviposition. The cultivars Atwalira, Nakyetengu and Muvubo with less oviposition preference are not the known resistant ones.

Similar results were obtained from the choice experiment. There were hardly any significant differences between cultivars regarding number of adults attracted to the cultivar and number of eggs oviposited (Figure 4.3).

Table 4.2. Analyses of variances for different trap catch variables (*=Significant at P=0.05)

Variable	Mean	F-value	P-value
Mean trap catches	2.87	1.42*	0.0467
Mean marked weevils	1.07	1.05	0.3962
Mean unmarked weevils	1.92	1.04	0.4081
Cumulative trap catch	5.56	1.29	0.1089

4.3.2 Antibiosis

4.3.2.1 Experiment 1 - Post embryonic development upto 15 days

In this experiment larvae were maintained up to the 15th day of development, whereafter the experiment was terminated due to high mortality rates. Data on larval weights, head capsule

Table 4.3. Number of eggs collected from a no choice experiment in which adult weevils were exposed to corm pieces of different cultivars for oviposition. Means (± SE) followed by the same letter are not significantly different at P > 0.05 (ANOVA F= 0.85; P = 0.6235).

Cultivar	Eggs
Gonja	17.9(±3.6) a
Nakitembe	15.7 (±2.7) ab
Nakabululu	15.1 (±3.2) ab
Nalukira	14.6 (±3.0) ab
Ndiizi	14.6 (±2.1) ab
Cavendish	13.6 (±2.7) ab
Kibuzi	13.6 (±2.3) ab
Yangambi-Km5	13.4 (±2.6) ab
Kabula	12.6 (±3.2) ab
Kayinja	12.1 (±1.8) ab
Mbwazirume	11.7 (±1.7) ab
Ndiibwabalangira	11.7 (±2.0) ab
FHIA-03	10.3 (±3.2) b
Atwalira	10.0 (±2.7) b
Nakyetengu	9.4 (±1.5) b
Muvubo	9.2 (±2.3) b
LSD (P 0.05)	*1.93*

size and estimates of larval stage are presented in Table 4.4. Although Mbwazirume ranked first in terms of larval weight and head capsule width, there were no significant differences between Mbwazirume and Gonja in the weight of larvae that developed. Generally resistant cultivars caused more than 50% mortality of larvae. However, Kibuzi and Ndiibwabalangira are susceptible EAHBs, but they also showed high larval mortality. There is however some

consistency of this result with known observations in which Atwalira, is known and considered susceptible, showing low mortality.

From estimated instar stages, it was clear that FHIA03 and Kayinja significantly increased the developmental time of banana postembryonic stages. In these two cultivars the larvae were still in third instar, whilst the larvae of other cultivars, especially EAHBs, were at seventh instar and almost pre-pupae (Table 4.4). Furthermore, after extraction, larvae from these two cultivars were weak and showed signs of reduced vigour.

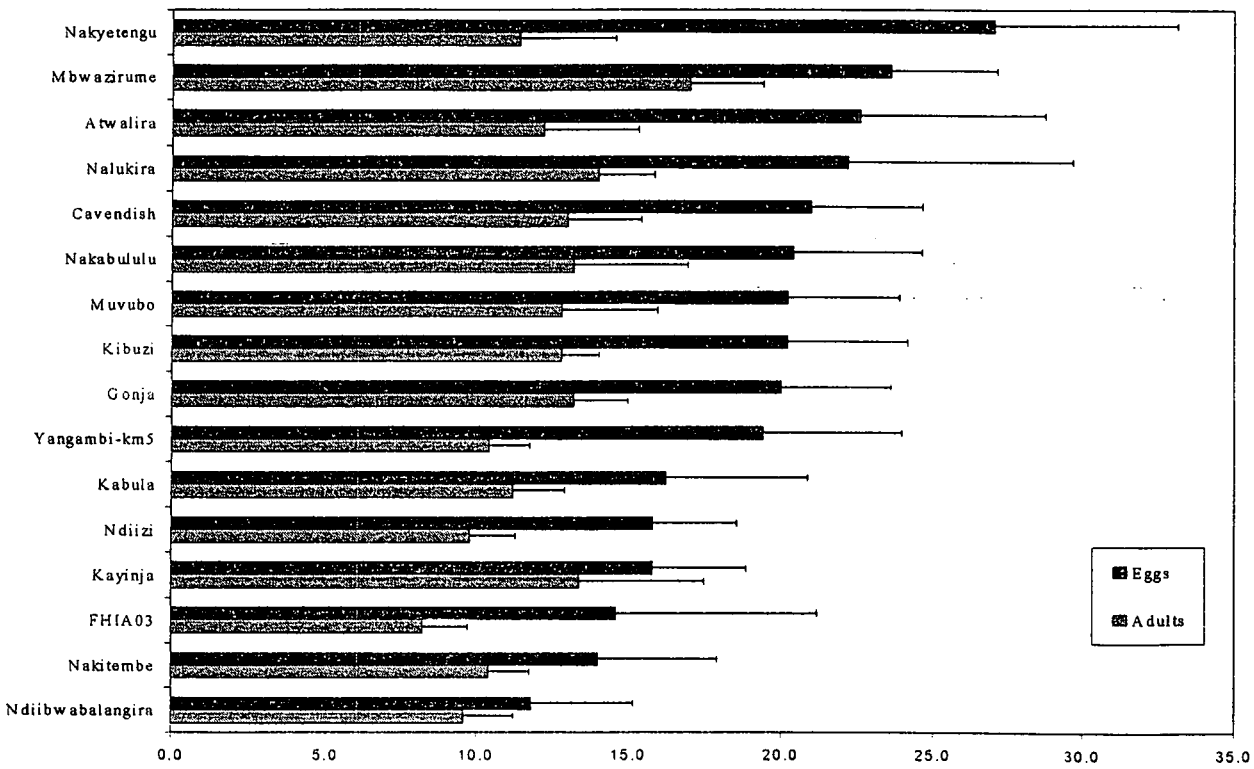


Figure 4.3. Number of adults and eggs collected from a choice experiment (error bars are standard errors)

4.3.2.2 Experiment 2 – Postembryonic development up to pupal stage

In experiment two, the number of larvae used was increased to 100 for each of the test cultivars so as to take the experiment up to pupae level. Data on pupae developmental periods and weights are presented in Table 4.5. By the end of the experiment all the immature stages

from Kayinja had died. High mortality was also experienced in Kabula and FHIA03. Mbwazirume, Ndiizi and Yangambi-Km5 also showed relatively high mortality of larvae.

Surprisingly Kabula, a brewing EAHB, was found to cause 90% mortality and significantly increase weevil developmental time, even though it showed field susceptibility in Chapter III. At the end of this experiment, there were no significant differences in pupal weight, but number of days to pupation was highly significantly different among cultivars. Yangambi-km5 caused a 40% increase in weevil developmental time compared to that of susceptible Gonja and other EAHBs (Table 4.5).

Table 4.4. Percentage mortality, mean larval weights, head capsule width in micrometer units (1 mu=0.0239 mm) and estimated instar stage following Gold *et al.* (1999a) of banana weevil larvae reared on corm material of different *Musa* cultivars.

Cultivar	Percentage Mortality	Larval weight (g)	Head capsule width	Estimated instar stage
Kibuzi	83	0.12 (±0.01)	96.0 (±1.9)	7
Kabula	77	0.04 (±0.01)	63.4 (±4.9)	4
Kisubi	77	0.06 (±0.01)	74.4 (±6.6)	5
KM5	67	0.11 (±0.02)	91.2 (±5.7)	6
Ndiibwabalangira	60	0.14 (±0.01)	96.6 (±2.4)	7
Ndiizi	60	0.06 (±0.01)	77.2 (±4.6)	5
Kayinja	50	0.02 (±0.01)	41.6 (±3.5)	3
Mbwazirume	37	0.16 (±0.02)	104.3 (±2.5)	7
Gonja	33	0.12 (±0.01)	102.4 (±2.4)	7
Nakyetengu	33	0.15 (±0.01)	98.9 (±2.9)	7
FHIA03	27	0.11 (±0.01)	53.1 (±3.2)	3
Atwalira	17	0.15 (±0.01)	102.8 (±1.6)	7
LSD (P=0.05)	-	*0.012*	*2.80*	-
ANOVA (P=0.05)	-	*F-value=9.08 P-value<0.0001*	*F-value=46.6 P-value<0.0001*	-

The non-significance of pupal weights from different cultivars has been observed in banana weevil by Silva and Fancelli (1998) and potato weevil (*Cylas puncticollis*) by Anota and

Odebiyi (1984). Increased developmental time could be an adaptation to attain an optimum required weight for pupation to take place. This means that there might also be no significant differences in the weights of the adults that emerge.

4.3.2.3 Experiment 3 – Postembryonic development in intact corms of different cultivars

In this experiment, it was observed that some cultivars encouraged larval development more than others did (Figure 4.4). For example, in Nakitembe and Muvubo most of the immature insects were pupae over the same developmental period, while in Nalukira, Ndiibwabalangira

Table 4.5. Percentage mortality, mean days to pupation and pupal weights of banana weevil pupa reared on corm material of different *Musa* cultivars

Cultivar	Mortality	Days to pupation	Pupal weight (g)
Kayinja	100	-	-
FHIA03	90	32.5 (±3.1)	0.064 (±0.014)
Kabula	90	37.8 (±0.5)	0.067 (±0.010)
Mbwazirume	78	33.4 (±0.7)	0.086 (±0.005)
Ndiizi	75	31.7 (±1.4)	0.084 (±0.010)
Yangambi-km5	75	39.6 (±0.9)	0.088 (±0.007)
Nakabulu	73	31.7 (±1.2)	0.063 (±0.007)
Nakawere	60	31.4 (±1.3)	0.093 (±0.005)
Nakyetengu	50	32.0 (±1.0)	0.067 (±0.005)
Nalukira	50	35.6 (±0.7)	0.095 (±0.004)
Cavendish	48	35.0 (±0.7)	0.084 (±0.003)
Tereza	48	31.0 (±0.7)	0.098 (±0.004)
Muvubo	45	30.6 (±0.2)	0.081 (±0.004)
Gonja	40	29.0 (±0.5)	0.077 (±0.006)
Kisansa	18	31.4 (±0.6)	0.073 (±0.004)
Ndiibwabalangira	5	31.2 (±0.9)	0.078 (±0.004)
LSD (P 0.05)	-	*0.67*	*ns*

and Mbwazirume, most of the immature insects were still larvae. At the other extreme, cultivars Yangambi-km5, Kayinja and FHIA03 yielded practically no larvae and pupae indicating that these cultivars did not support development. Mbwazirume and Ndiizi showed

some level of resistance, with low levels of both pupae and larvae. It has been observed in results from the field screening trial (Chapter III), that Mbwazirume is relatively resistant.

4.3.2.2 Experiment 4 – Effect of sap on egg hatchability

Sap or latex that exudes from banana plants apparently shows some effect on the survival of banana weevil eggs and larvae. Chemically sap has been found to be rich in ions especially

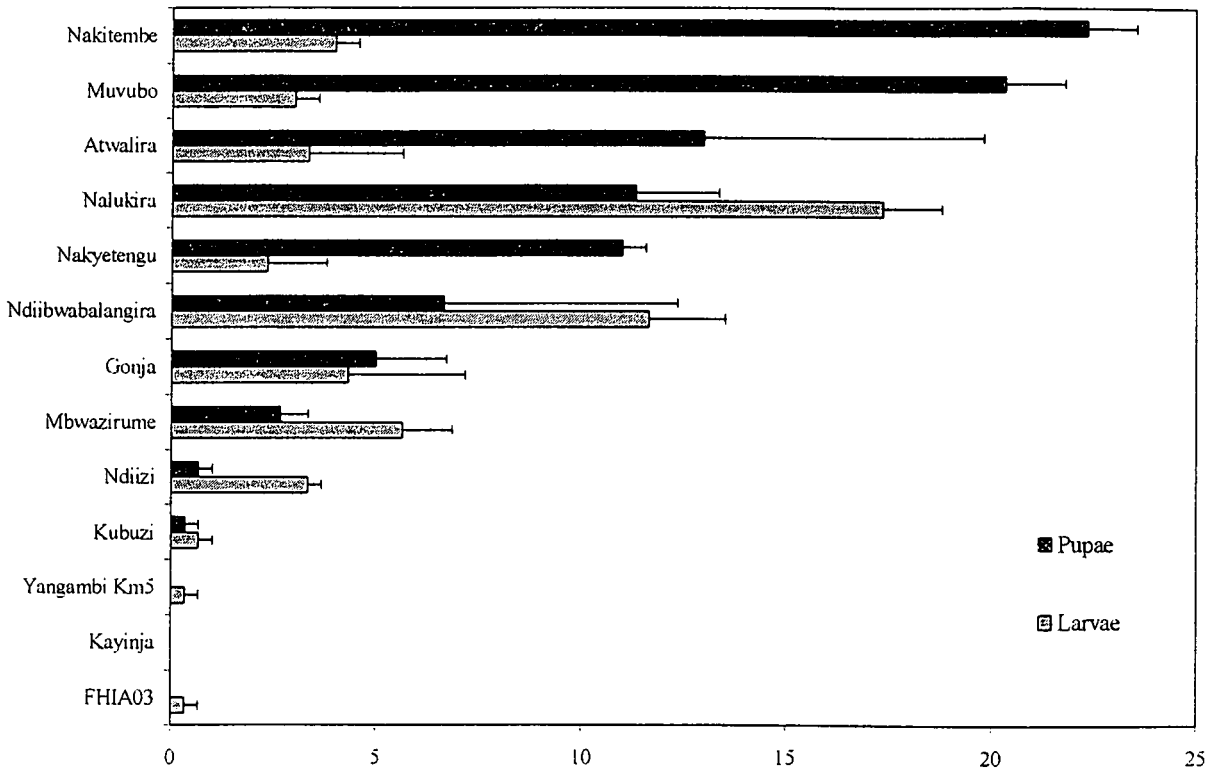


Figure 4.4. Number of immature stages collected after 27 days of development on corms of different *Musa* cultivars. The cultivar names are sorted on number of pupae whose ANOVA was significant at $P > 0.05$ ($F=8.84$, $P<0.0001$)

K+, Mg2+, Cl-, and NO3- (Baker *et al.*, 1990). These, plus other inclusions like globular vesicles and crystalloid vesicles have been found to be osmotically active (Kallarackal *et al.*, 1986). These ions and inclusions may have either acted as desiccants or toxins to the eggs. When weevil eggs were exposed to sap/latex freshly collected from different cultivars, there were significant differences in the hatchability of the eggs (Table 4.6). Although the hatchabilities were still high, FHIA03 followed by Yangambi-Km5 caused the highest

reduction in hatchability compared to the other cultivars tested. Even in the control where distilled water was used, five percent did not hatch (Table 4.6).

Table 4.6. Hatchability (%) of banana weevil eggs incubated in contact with sap/latex collected from 13 *Musa* cultivars. Means (± SE) followed by the same letter are not significantly different ($P < 0.05$) ANOVA $F=4.04$ and $P=0.0003$

Cultivar	Percentage Hatchability
Control (dist H_2O)	95 (±1.0) a
Ndiizi	90 (±2.6) ab
Cavendish	89 (±1.0) ab
Nakitembe	89 (±3.0) ab
Nakyetengu	89 (±1.9) ab
Nakabululu	88 (±1.6) abc
Nalukira	88 (±1.6) abc
Gonja	86 (±2.6) abc
Mbwazirume	86 (±2.6) abc
Ndiibwa	85 (±3.4) abc
Kabula	83 (±5.7) abc
Kayinja	75 (±3.8) bc
FHIA03	72 (±3.7) bc
Yangambi-km5	74 (±6.6) c

4.4 Discussion

This study has found very little differential attraction of weevils to host plants of different cultivars in the field. This is in support of other studies by Pavis and Minost (1993) and Musabyimana (1995) who did not find any relationships between attraction and weevil damage. Although studies by Buddenburg *et al.* (1993) found that banana plants emitted a volatile substance which attracted weevils to host plants, and other studies found higher feeding stimulants in susceptible cultivars than resistant ones (Rwekika, 1996). This discrepancy may be due to different dispersal mechanisms in the field as opposed to the

laboratory where weevils are attracted towards pure volatiles. Further more, volatilies are emitted in high quantities by freshly cut or wounded plants, which is not the case with intact plants in a normal field situation.

Under laboratory conditions, there was almost no differential attraction and ovipositional preferences on corms of susceptible and resistant cultivars. The few significant differences that do exist were inconclusive because they did not reflect the known resistance responses. Abera (1998), found similar results when she observed higher oviposition on resistant Kayinga cultivar than the susceptible EAHBs. With the relatively good consistency of results from other studies and this one, it would be safe to say that antixenosis is not an important resistance mechanism in banana weevil.

Adult weevils are known to prefer highly moist environments (Rukazambuga, 1996) and attraction may be driven by such factors rather than preference for feeding or oviposition. Therefore, the slight differential attraction to some cultivars may probably be due to such factors as microclimate. If this analogy is true then one should find higher aggregation on mats with higher biomass, canopy cover (functional leaves) and suckering, since these encourage a cooler and wetter microenvironment suitable for weevil presence. Attractants emitted from host plants may be important in assisting to locate a suitable environment, followed by aggregation for mating, feeding and then oviposition, irrespective of the cultivar of the host plant. Resistance then operates after ovipostion.

It would be difficult to imagine that weevils, which are so small compared to their host and with slow and limited movement (Gold *et al.*, 1998), can walk around the field selecting which plant to oviposit on. More studies on weevil movement are underway at IITA-ESARC, but unless it is found that these weevils can disperse and locate hosts by flying, it would be unrealistic to suppose that they walk around a 1-2 hectare plantation looking for a suitable host plant.

Results of weevil growth, development and survival indicate that resistant cultivars may contain substances that are antibiotic to banana weevil. Kayinja, Yangambi-km5 and FHIA03 have consistently shown that banana weevil larvae do not develop well in their corms. This is reflected in the low survival rates, lower body weights and size plus significant increase in

developmental time of larvae developing in these resistant cultivars. These results are consistent with that of Lemaire (1996), who found that Yangambi-km5 significantly increased developmental time of weevil larvae. Sap and latex showed some effect on the survival of weevil eggs, but more work needs to be done on this aspect. Observations were made with the help of a binocular microscope and these revealed that after hatching the young and delicate first instar larvae become entrapped on the surface of the sap and were inhibited from moving for days, probably leading to starvation and ultimate death.

This study suggests that resistance in banana is mainly under the control of antibiotic factors. These factors may be of a different nature in the various cultivars. It has already been seen in Chapter III that corm hardness showed a small but significant negative correlation with damage. Tissue hardness may be an antixenotic factor, but in banana where gravid females do not seem to select the type of host on which to oviposit, it becomes an antibiotic mechanism because it operates after selection. There is therefore little doubt that antibiosis is the only way in which banana host plants can resist attack by weevils and it must be components present inside the tissues of resistant cultivars, which are the major factors in varietal resistance of *Musa* to banana weevil.

CHAPTER V

CHEMICAL BASIS OF RESISTANCE TO BANANA WEEVIL (*COSMOPOLITES SORDIDUS* GERMAR) WITHIN *MUSA* GERMPLASM IN UGANDA.

5.1 Introduction

The acceptance of phytophagous insects to utilise a host plant depends on both the biophysical and chemical features of the plant. These features may be localised in different parts of the plant and this may be the reason why most species of insects are confined to certain plant parts. Chemical factors of plants have been found to be very important in host selection by phytophagous insects and the narrow host range of most phytophagous insects depends largely on the presence or absence of a variety of secondary metabolites, as well as nutrients (Bernays and Chapman 1994).

The first plant chemicals insects encounter before reaching the host plant are volatile molecules. Budenberg *et al.* (1993) and Ndiege *et al.* (1996) studied volatile components released by banana plants and found a series of mono- and sesqui-terpenes that were important in attracting weevils. They suggested that these chemicals would play an important role in aggregation as a complement to pheromones and in the orientation of weevils to the banana plant for feeding and oviposition.

On arrival at the host plant, insects encounter surface compounds present in wax and cuticles. Although there are no reports on banana surface waxes and cuticles, it is likely that banana plants release volatiles through these surface structures. Most of the studies, however, report that volatiles are released from freshly cut or wounded plants rather than intact plants. Adult banana weevils have been reported to feed on dead plant material (Simmonds, 1966). Therefore, attraction to fresh banana plants may be for mating-aggregation and oviposition where females oviposit their eggs in small holes made into the plant tissue by using their rostrums. This directly exposes eggs and larvae to internal compounds, which may influence hatchability and larval development. Internal compounds may be divided into two types, nutrients and secondary metabolites. Rwekika (1996) studied feeding allelochemicals in adult banana weevil among several cultivars. He found that methanol and water extracts of

susceptible cultivars induced higher feeding than extracts of the resistant cultivars. He went further to identify and isolate a compound salicin, which elicited the highest feeding response. He also found that sugars fructose and glucose were also important feeding stimulants and that susceptible cultivars contained higher amounts of both salicin and glucose.

Studies on secondary metabolites that affect insects have gained interest and momentum in the last several years. Several techniques can be used for identification and quantification of chemical components in plants and High Performance Liquid chromatography (HPLC) is perhaps one of the most modern, quick and accurate methods (Bidlingmeyer, 1992). HPLC is an analytical separation technique, whereby a mobile liquid and a stationary solid phase effects the separation of molecules, due to their different absorbency rates. As the sample moves through a packed column, the absorbency of each component is detected by an ultraviolet or infrared detector set at a particular wavelength. The detected components are then displayed graphically as peaks on a chromatogram. In this study, an attempt was made to investigate the presence of active compounds in corms of resistant cultivars that may be responsible for the observed weevil larvae mortality in laboratory bioassays and to test crude extracts that may show active components against banana weevil.

5.2 Materials and methods

HPLC was used to separate methanol extracts of corms of different cultivars into individual compounds indicated by peaks on a chromatogram. These peaks were tested for relationships with weevil response among selected cultivars. After identification of differences related to weevil damage, crude extracts were tested in a bioassay to determine their effect on hatchability and early larval development.

5.2.1 High performance liquid chromatography (HPLC)

Fifteen cultivars were selected based on results of the preliminary field screening experiment to represent three weevil response groups (levels). The groups represented resistant, intermediately resistant and susceptible cultivars based on total inner damage.

5.2.1.1 Collection of samples

From the screening trial (Chapter III), about 25 g of fresh corm material was collected from medium sized plants (about 2 m tall) of 15 cultivars selected to represent three banana weevil damage groups. Care was taken to take a bit of both the outer cortex and inner central cylinder material. The samples were replicated three times (a sample from three different plants of the same cultivar).

5.2.1.2 Extraction

Extraction was done by grinding 25 g of corm material in 50 ml of methanol and left covered to extract for 24 hours. The samples were then filtered once using Wattman No. 4 filter paper, and the filtrate concentrated to 10 ml using a BUCHI (RE11) Rotervapor evaporator.

5.2.1.3 HPLC condition

The column used was a BECKMAN Ultrasphere (ODS 5 4.6 mm x 25 cm) at a flow rate of 1.0 ml per minute on a System Gold 126 HPLC machine. The pressure was 1.6 KPSI and temperature normal (23-25°C). The detector was a System Gold 168 set first at 215 nm and then at 323 nm. The mobile phase was set at the gradient shown in the programme in Table 5.1.

Table 5.1. HPLC programme for the separation of methanol extracts of banana corms used for both 215 nm and 323 nm detection wavelengths

MeoH (%)	H_2O (%)	Time (min.)
0	100	3
30	70	2
75	25	10
100	0	5
0	100	

During the analysis, 20 µl of each sample was injected and run through the HPLC at the conditions specified above. The profiles of compound peaks produced by the detector were printed in the chromatogram. Data on peak height, elution times and percentage area under the peak was downloaded. The procedure was repeated with the detector set at 323 nm.

5.2.1.4 Data analysis

From both the 215 nm and 323 nm chromatograms, major peaks were identified, numbered and their percentage areas analysed, using k-means clustering in STATISTICA for Windows 5.0 (StatSoft, 1995). Clustering was done to group cultivars into categories depending on presence and quantities of different active compounds so that comparisons between these categories and banana weevil damage could be made. Pearson's correlations were performed on all peaks plus banana weevil damage values from the field screening experiment in Chapter III.

5.2.2 Bioassay of crude methanol extracts

From the results of the HPLC analysis some resistant cultivars were observed to contain compounds that were absent in the susceptible ones. It was decided to investigate the effects of the crude methanol extracts of one of the resistant cultivars on hatchability and early development of banana weevil larvae. Three cultivars were selected, Kayinja, a resistant cultivar showing presence of 'resistance' compounds, and two EAHB cultivars Musakala and Atwalira which are susceptible and without 'resistance' compounds. For each cultivar, extractions were made by grating 100 g of fresh corm material in 100 ml of methanol. The mixture was left to extract for 24 hours and then filtered with Wattman No. 4 filter paper. Corn meal agar media for each cultivar was prepared by adding extract to water at a ratio of 1:25 (1 ml of extract to 25 ml of water) and adding 0.017 g of agar to each millilitre of extract and water mixture. The mixture was autoclaved for 15 minutes at 120 °C. Liquid agar medium was poured into sterile petri dishes and left to cool. After sufficient cooling 25 five-day-old eggs were placed on the medium after washing them in 40% ethanol solution and left to incubate. Hatchability and percentage tunneling was recorded over a four day period.

5.3 Results

5.3.1 HPLC

Cluster analysis performed on the selected peak areas of the components resulted in three clusters as shown in Table 5.2. Most cultivars in cluster one are susceptible, with the exception of Yangambi-km5 and Cavendish. Cluster two has only three members;

Nakabululu, Nalukira and Nakyetengu, of which Nalukira and Nakyetengu are known to be moderately resistant. Members of cluster three are known to be resistant to banana weevil as indicated by the corresponding damage values in Table 5.2. The presence of Yangambi-km5 and Cavendish in the susceptible cluster is an indication that some other mechanisms, rather than their chemical content, may be important for resistance in these two cultivars. From experience it is known that these two cultivars have hard corms, making tissue hardness an important factor. Kayinja, FHIA03, Calcutta-4 and TMB2x7197-2 are resistant and have some peaks in common, which may represent compounds detrimental to the development of banana weevils and which are thus important resistance factors.

Table 5.2. Cluster groups of cultivars based on peak variables from the 215 nm and 323 nm chromatograms. PCI = Percentage coefficient of infestation

Cluster	Name	Total inner damage	PCI
1	Kibuzi	10.1	19.9
	Nakawere	8.8	19.3
	Obino L' Ewai	8.3	20.8
	Musakala	6.5	18.2
	Kabula	3.1	14.0
	Tereza	3.0	14.7
	Cavendish	1.7	8.0
	Yangambi-km5	0.3	2.1
2	Nakabululu	6.4	17.4
	Nakyetengu	4.1	10.7
	Nalukira	3.1	10.7
3	Kayinja	2.4	9.9
	FHIA03	2.2	9.6
	Calcutta-4	0.2	1.7
	TMB2x7197-2	0.1	0.6

From Figure 5.1 it can be observed that peaks P215_3, P215_4 are present only in the resistant cultivars apart from P215_3 in Nalukira which is intermediately resistant. Peaks

P215_6, P215_7, P215_8 and P215_9 are present in all cultivars, but with higher relative concentrations in the resistant cultivars than the susceptible ones. In Figure 5.2 peaks P323_2, P323_8, P323_10 and P323_14 showed the highest relationships with weevil damage (Table 5.3).

Table 5.3. Correlation matrix of major HPLC peaks and key banana weevil damage variables (* = Coefficients are significant at $p < 0.05$)

	P215_4	P215_6	P215_7	P215_8	P215_9	P323_2	P323_8	P323_10	P323_14	PCIU	PCIL	PD	PXI	PXO	TD
P215_3	0.94*	0.35	0.61*	0.37	0.78*	-0.73*	-0.40	-0.71	-0.69	-0.59*	-0.57	-0.54	-0.51*	-0.55*	-0.55*
P215_4		0.40	0.60*	0.51	0.79*	-0.66*	-0.35	-0.68*	-0.64*	-0.52*	-0.49	-0.48	-0.45	-0.48	-0.48
P215_6			0.20	0.73	0.24	-0.12	-0.52	-0.12	-0.36	-0.56*	-0.55*	-0.52*	-0.38	-0.43	-0.42
P215_7				0.47	0.66	-0.46	-0.47	-0.68	-0.49	-0.73*	-0.74*	-0.75*	-0.69*	-0.73*	-0.74*
P215_8					0.49	-0.06	-0.58*	-0.34	-0.34	-0.55	-0.52	-0.52	-0.54*	-0.49	-0.53
P215_9						-0.68	-0.39	-0.83	-0.48	-0.74*	-0.72*	-0.68*	-0.58*	-0.66*	-0.65*
P323_2							0.38	0.57	0.49	0.54	0.48	0.51	0.61	0.51	0.58*
P323_8								0.37	0.37	0.63	0.59	0.55	0.70	0.48	0.60*
P323_10									0.56	0.72*	0.70*	0.63*	0.52*	0.60*	0.58*
P323_14										0.54	0.51	0.57	0.47	0.62*	0.57*
PCIU											0.99*	0.97*	0.79*	0.89*	0.88*
PCIL												0.96*	0.74*	0.88*	0.85*
PD													0.83*	0.97*	0.94*
PXI														0.87*	0.96*
PXO															0.97*
TD															

PCIU = Percentage coefficient of infestation (upper position)
PCIL = Percentage coefficient of infestation (upper position)
PD = Peripheral damage
PXI = Percentage cross-section damage (inner)
PXO = Percentage cross-section damage (outer)
TD = Total inner damage.

Some significant correlations were observed between major peaks and banana weevil damage indices (Table 5.3). Peak P215_7, for example, was negatively correlated to all damage indices by more than –0.65, while peak P215_3 was negatively correlated to PCI (upper) and total inner damage by –0.59 and –0.55 respectively. The relationship was also high for other damage indices. Peak P215_9 is also significantly negatively correlated to PD and total inner damage by –0.68 and –0.65 respectively. These peaks represent compounds or substances that may be detrimental to weevil development in 50-70% of the cultivars used in this study.

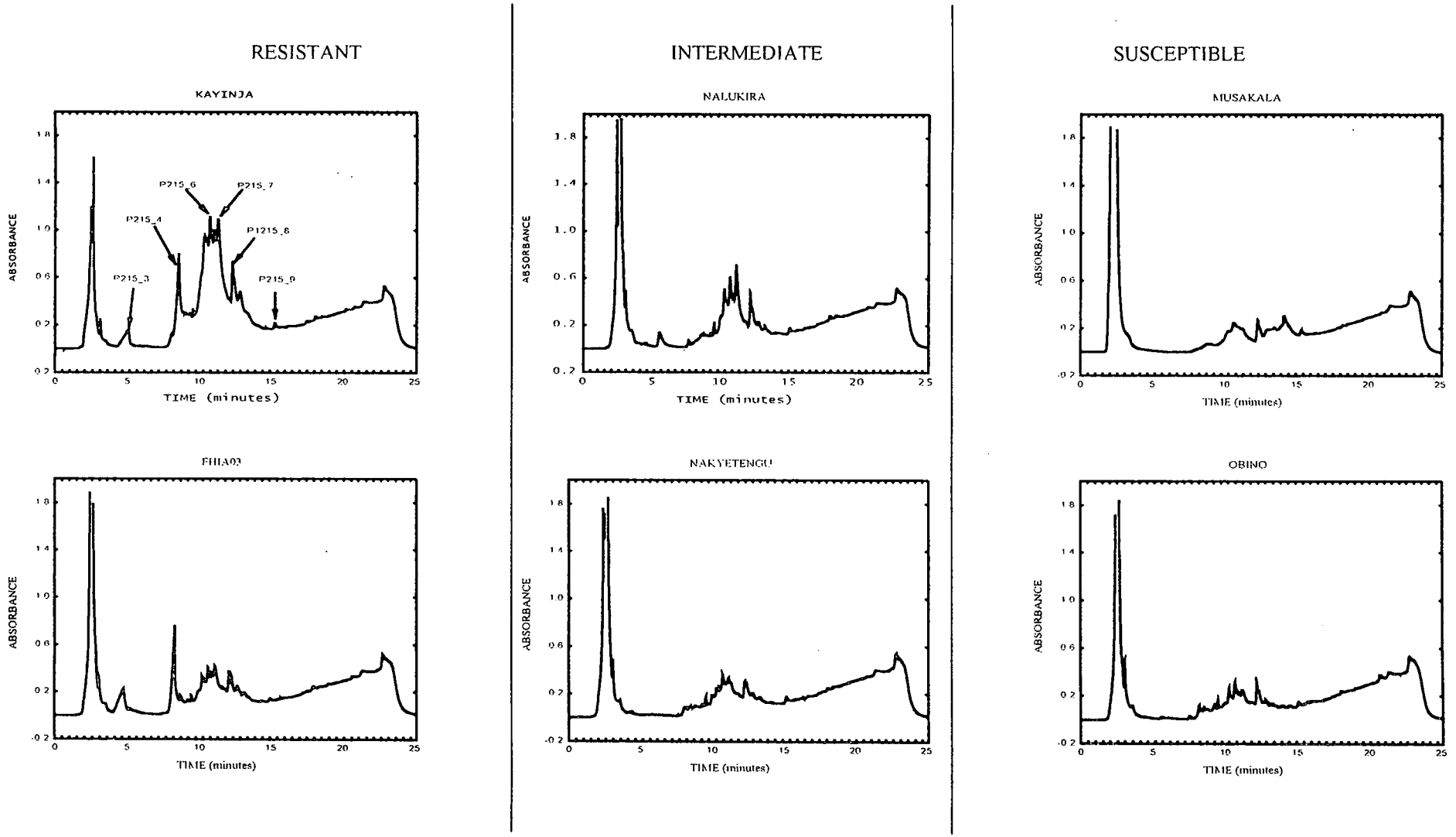


Figure 5.1. Representative HPLC chromatograms (detector set at 215 nm) of methanol extracts from selected *Musa* cultivars showing differences in peaks of active compounds and cultivar response to banana weevil

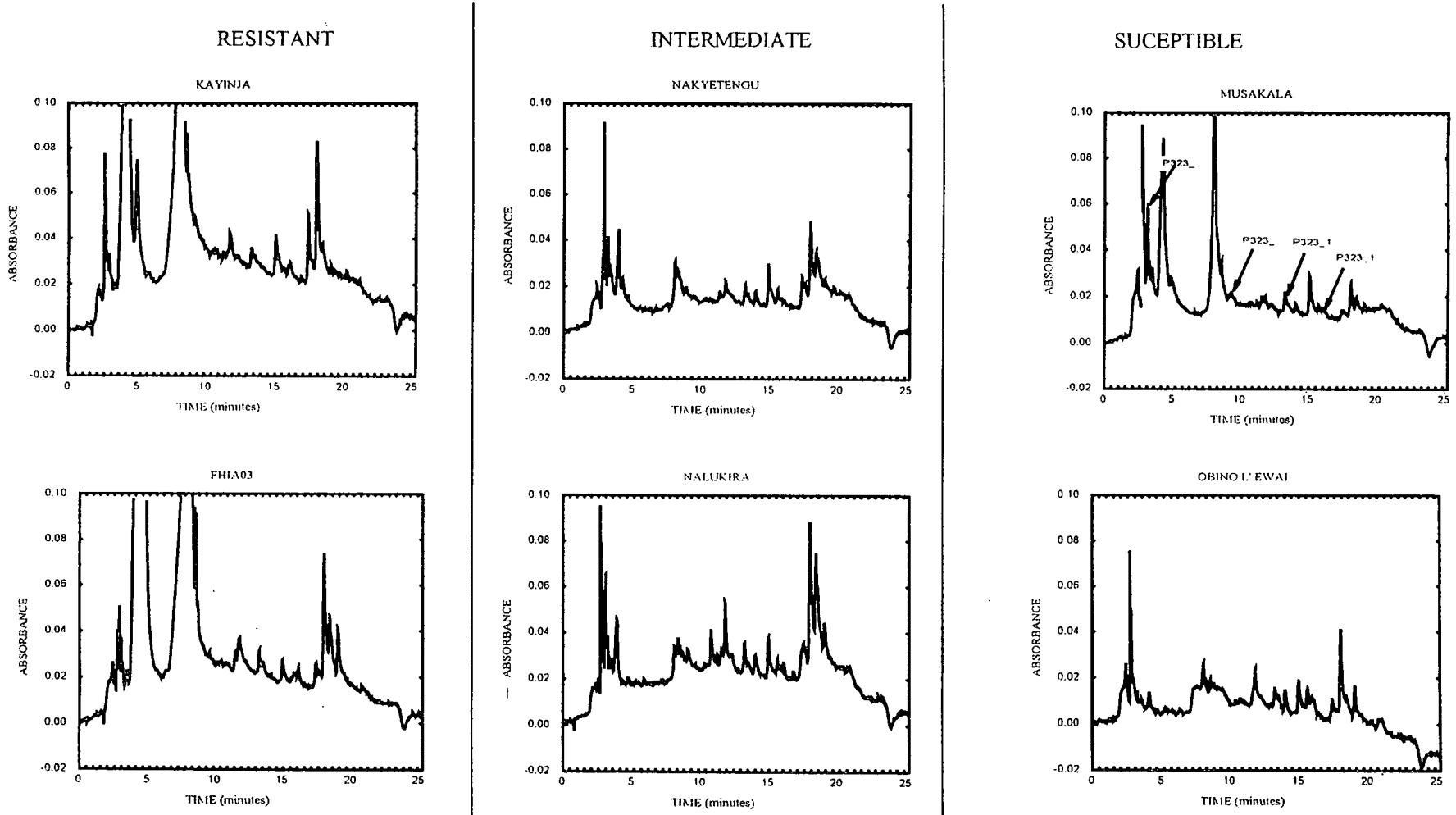


Figure 5.2. Representative HPLC chromatograms (detector set at 323 nm) of methanol extracts from selected *Musa* cultivars showing differences in peaks of active compounds and cultivar response to banana weevil

Future work should target these compounds for identification, isolation and testing. Peaks P323_8, P323_10 and P323_14 that are positively related to some weevil damage variables (*e.g.* PCI upper, r=0.72; PD, r=0.63 and TD r=0.5) may represent feeding stimulants, encouraging weevil feeding and development.

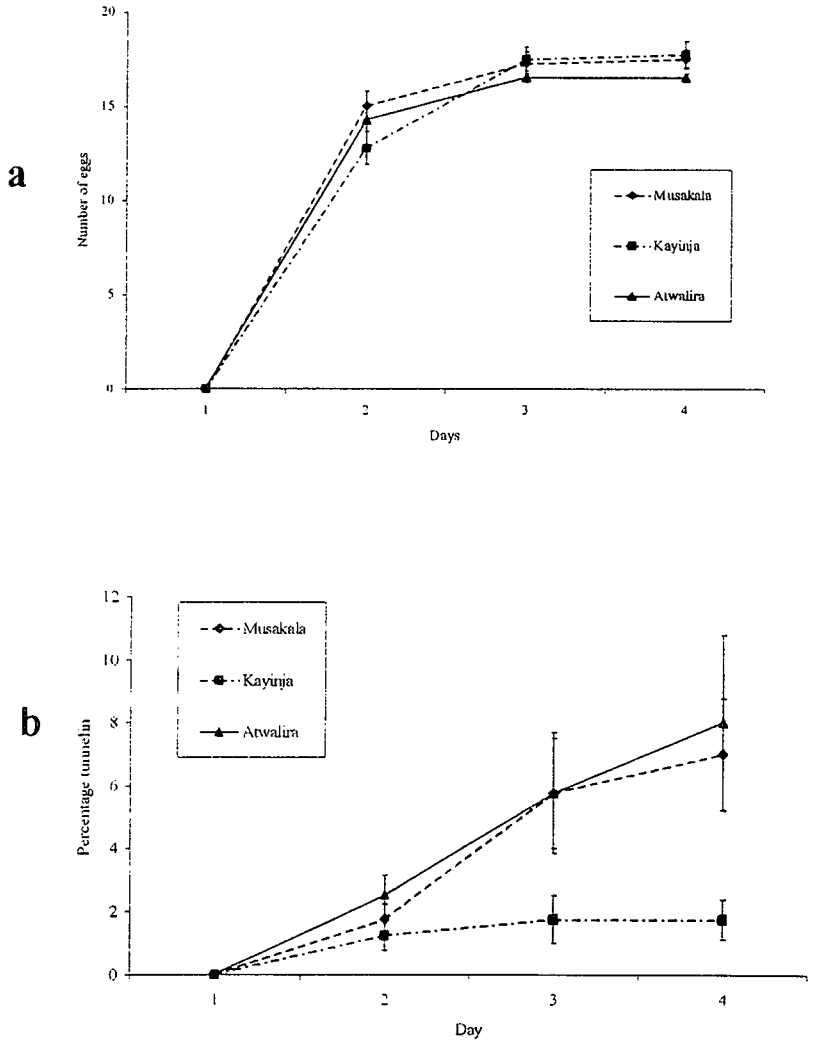


Figure 5.3. a. Hatchability of weevil eggs incubating on corn meal agar with crude methanol extracts of three different *Musa* cultivars.

b. Percentage tunneling of weevil larvae after hatching on corm meal agar containing crude methanol extracts of three different *Musa* cultivars.

5.3.2 Bioassay of crude methanol extracts

Results of the bioassay indicate that compounds present in methanol extracts of Kayinja and probably other cultivars with similar peak profiles affect the development of weevil larvae. Whereas there were no significant differences in hatchability (Figure 5.3A), there was a significant difference in percentage tunneling (Figure 5.3B), which is a measure of activity. Larvae tunneling in the agar containing Kayinja extract were observed to be very slow and by the 3rd day, the larvae had altogether stopped tunneling. Larvae in agar containing extracts from the other susceptible cultivars, were still actively tunneling and developing after the 3rd day (Figure 5.3B).

5.4 Discussion

This study has established that some resistant cultivars contain compounds that might be important as antibiotic resistance factors against banana weevil. From observation and analysis of the chromatographic data, resistant cultivars show peaks of active compounds that are absent in susceptible cultivars. At the same time some compounds which appear to be present in susceptible cultivars are absent in resistant cultivars. Could these be the feeding stimulants isolated by Rwekika (1996)?

It is interesting to note that some resistant cultivars (Yangambi-km5 and Cavendish) did not show compounds active against banana weevil and it may be assumed that in these cultivars other mechanisms of resistance are important. Corm hardness, which has been observed in these two cultivars, may be their means of resistance to banana weevil.

Laboratory bioassays using crude extracts have shown significant effects on the early development of banana weevil larvae. Since the extracts are from methanol (a polar solvent), it means that the active compounds are also polar in nature. This offers a real possibility for using these in the control of banana weevil and screening large segregating populations as markers for resistance in a breeding programme. HPLC may be a promising technique for quickly identifying and quantifying such compounds. It is therefore proposed that further work should be undertaken to identify, isolate, and test the compounds whose peaks have been observed to contribute to resistance in this study.

CHAPTER VI

GENERAL DISCUSSIONS

"The host plant of a phytophagous insect is the universe in which the insect derives nourishment and shelter" (Kogan 1982). The banana weevil depends solely on *Musa* and *Ensete* host plants for reproduction and thus the survival of its species. This close association must have evolved over a long evolutionary period. Humans are, however, interested in finding ways to reduce the destruction weevils do to the banana crop. In this way, better food security can be ensured in the communities that depend on banana for food. One of the most basically important and cost effective ways to control crop pests is the selection and development of resistant cultivars.

The literature review in Chapter II has shown some advances in the search for resistance among *Musa* germplasm in different regions. Unfortunately the study reports found are fragmented and some of the results inconsistent. Additionally it becomes difficult to compare these results because the conditions and cultivars used in the studies were different. Nevertheless some conclusions can be drawn. For example it is clear that plantains are the most susceptible *Musa*, subgroup while Pisang-Awark and Bluggoe cultivars are resistant. Although some cultivars have been identified as potential sources of resistance, the mechanisms involved in resistance were still not clearly understood.

It is also fairly agreed upon in the literature that non-preference or antixenosis is not important as a resistance mechanism in banana weevil resistance. Studies on attraction of the weevils to plants have failed to find any relationships between attraction and damage.

In this study, more pieces are added to the puzzle of host-plant interactions, mechanisms of resistance and some genetic implications these may have towards the development of resistance cultivars. It is evident from this study that resistance to banana weevil in *Musa* is a complex trait and this is in agreement with Ortiz *et al.* (1995). Although all factors could not be studied, observations indicate that several factors were important in banana weevil resistance.

In Chapter III of this study, a large number of *Musa* germplasm was screened against banana weevil and some genetic components for characters related to banana weevil resistance and other important agronomic traits were analysed. The screening experiment revealed differences among genome groups and, as expected, plantains followed by EAHB showed highest susceptibility. Although Calcutta-4 is a highly resistant wild banana, its resistance genes could not be transferred sufficiently into the plantain tetraploid hybrids studied. This is shown by tetraploid hybrids, TMPx5511-2, TMPx7002-1 and TMPx7152-2 remaining quite susceptible. In the IITA plantain breeding programme, these hybrids were obtained by crossing triploid plantains (Obino l'Ewai and Mbi Egome) with pollen from the highly fertile wild diploid Calcutta-4 (Vuylsteke *et al.*, 1993). The tetraploid hybrids are believed to have originated from the fertilisation of unreduced triploid female gametes during meiosis, recombination thus occurring only in the diploid male parent. The results of these tests indicate that this may be true and that the tetraploid hybrids retain the susceptible characteristic because they contain the full genomic constitution of their female parent. This is probably what Ortiz *et al.* (1995) referred to as dosage effects of the banana weevil susceptible gene in plantains.

The ABB bananas (Kayinja and Bluggoe) showed highest resistance and as we shall see later, antibiotic resistance to banana weevil seems to be resident on the B genome. There also seems to be a dosage effect for resistance on the B genome because this resistance is not observed in plantains, which are AAB and yet FHIA03 with genome AABB is highly resistant. This implies that the B genome must be present twice (or more than once) for it to confer resistance as in Kayinja and Bluggoe (ABB).

Its is interesting to note that differences were also observed within the EAHB. Chapter III shows that cultivars Mbwazirume, Tereza, Nalukira, Nsowe and Nakyetengu are the most resistant EAHBs. Two of these, Nalukira and Nsowe, are brewing types and not considered very important. Tereza, was until recently a little known accession maintained in the germplasm, but when it produced some of the highest number of seeds after crossing it with Calcutta-4, it has since become an important EAHB female parent (Ruth Ssebuliba[3], *personal communication*). Mbwazirume and Nakyetengu are two very important cultivars in Uganda. Although they belong to different clone sets (Nakitembe set and Nakabululu set for

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Mbwazirume and Nakyetengu respectively) (Karamura, 1998), they are both characterised by thick pseudostems. Nakyetengu is the shortest of all EAHB and has been selected for resistance to wind damage, especially in western Uganda (Kabarole District), while Mbwazirume is of medium height. They are well adapted to many environments, and produce fairly large bunches, which also make good 'Matooke'. These may be the reasons both cultivars are well distributed throughout the banana growing regions of Uganda. Their synonyms have also been reported in western Kenya and Northwestern Tanzania (Deborah A. Karamura, *personal communication*). In this study they have shown resistance to banana weevil, while work on resistance to nematodes also revealed that among the EAHBs, Mbwazirume was most resistant (Speijer *et al.*, 1998). Unfortunately Mbwazirume is completely sterile (Ruth Ssebuliba, *personal communication*) and may not be considered an important source of resistance in a breeding programme, unless it can be found to have some male fertility.

Yangambi-km5 and Cavendish (both AAA), although without a B genome, are highly resistant cultivars and as already noted, their mechanism of resistance may be completely different from that of the other resistance cultivars that have the B genome. These two cultivars, together with FHIA03 and three selections from the IITA hybrids, *i.e* TMB2x8075-7, TMB2x7197-2 and TMB2x6142-1, may be important sources of resistance and should be included into breeding programmes for banana weevil resistance.

From the genetic analyses carried out in this study, the most important characters measuring banana weevil resistance and other agronomic traits have fairly high genetic control as shown by the clonal heritability estimates (Chapter III). Plant girth, which showed the highest heritability of 99%, has previously shown to correlate significantly with yield in terms of bunch weight, and models have been derived to predict yield before flowering based on the girth of the plant (Bosch *et al.*, 1995). Total inner damage, which was developed by Gold *et al.* (1994b) and used here for the first time as a banana weevil screening measure, scored a heritability of 87%. This means that 87% of the variation observed in this trait is genetically controlled and most importantly, the use of this measure as a basis for screening and selection would make the best progress compared to all the other indices, such as PCI, which has been used in the past. PCI variables in this study scored heritabilities ranging from 47% to 55%. High genetic correlations were observed between all weevil variables, an indication that only one would suffice as a good measure in the future. Again total inner damage was found to

have genetic correlations of very close to unity for all damage indices scored. This further supports the suggestion that it is the most important weevil damage indicator.

During this screening trial several plant factors were considered in order to determine their relationship to weevil damage. The relationships were different when different groups of cultivars were analysed separately, indicating that resistance factors are dependent on the *Musa* subgroup. However, it can be summarised that number of days to flowering is significantly negatively correlated with PCI upper, PCI lower and percentage peripheral damage (r values -0.57, -0.48 and -0.46 respectively). The implication of these correlations is still not clear, but it is assumed that time to flowering represents the period during which the plant accumulates more dry matter which is important in resistance as was observed in Chapter III. Corm hardness influenced resistance only within exotic cultivars. From Chapter III, peripheral corm hardness was negatively correlated with PCI upper, PCI lower and percentage outer damage (r values -0.31, -0.23, and -0.26 respectively). Although these coefficients are small, they were significant, an indication that in a few cultivars hardness of corm tissues is important. Outer dry matter content had a wider influence and it was negatively correlated with PCI upper, PCI lower, percentage peripheral damage, percentage outer damage and total inner damage. (r values -0.68, -0.65, -0.59, -0.50 and –0.37 respectively), indicating that since problems were experienced with measuring hardness, dry matter content can be an indirect measure of tissue hardness. Resin/sap content also showed some relationships with weevil damage. It was correlated with PCI upper, PCI lower, percentage peripheral damage, percentage inner damage, percentage outer damage and total inner damage (Table 3.11a) (r values -0.40, -0.38, -0.36, -0.20, -0.33, and -0.28 respectively). Corm size (cross section diameter) has also shown relationships with banana weevil damage. Within EAHBs outer diameter of the upper position, for example, was negatively correlated with percentage inner damage, percentage outer damage and total inner and damage (r values -0.53, -0.41, and -0.51 respectively). This means that smaller plants suffer higher internal damage as weevil larvae can penetrate deeper and get to the central cylinder faster. This is in agreement with Balachowsky (1963) who proposed that the large corm displayed by Gros Michel was an important resistance mechanism. Within EAHBs there was a very small, but significant, relationship between suckering ability and weevil damage. From Table 11b suckering ability is negatively correlated with percentage inner, outer damage and total inner damage (r values -0.30, -0.30 and -0.32 respectively). This agrees with Mesquita *et al.* (1984) who suggested that higher suckering ability reduces damage to the mother plant as the young

suckers growing around fend it from fresh attack. Alternatively, fresh and active growth characterised by suckers may attract weevils away from older mother plants.

Painter (1951) was the first to partition resistance against insect pests into three categories. He suggested that resistance whereby an insect is retarded from using a particular type of host plant be regarded as 'non-preference'. This was later changed to antixenosis to reflect the response by the host plant. Then if an insect pest accepted a particular host plant but later suffered biologically in terms of reduced development, poor health and fitness or even death, this type was referred to as antibiosis. The last category Painter (1951) referred to as tolerance, whereby a particular type of host plant can support a number of insect pests which would cause damage in another type of the same species. This study did not investigate tolerance because it would require a completely different experimental trial. Antixenosis was not found to be an important mechanism in the *Musa* germplasm studied here. Studies on field trapping at the base of each plant and laboratory choice bioassays did not show significant differences among cultivars for preference. This is in agreement with Fogain and Price (1994), Pavis and Minost (1993), Musabyimana (1995), Lemaire (1996) and Abera (1998). All these authors found no relationship between attraction and damage and/or ovipositon. Although plant volatiles are known to attract weevils (Treverrow, 1990), they are released mostly from cut or wounded plants. They may be more important for aggregation, at times when pheromones are not present (Ndiege *et al.*, 1996) and to help the weevil orient towards the host plant for moisture which they are very attracted to. Ittyeipe (1986) found that weevils were attracted towards banana corm material in an arena only if the material was moist. In his experiments, after some days, weevils ended up moving towards potatoes and yams which were rotting and producing a lot of moisture compared to the then dry banana corms. Studies on banana weevil movement patterns have revealed that weevils are generally sedentary with very limited movement. Clifford S. Gold and Godfrey Kagezi[4] (*unpublished data*), for example, found that after 7 days 75% of previously released weevils had not moved, while 17% had moved only 9 m in a mulched garden. Movement was higher in a non-mulched garden. Apparently weevils fly very rarely and it is difficult to imagine them, so small in size compared to the host plant and with their very slow movement patterns to be able to move around on a one acre plot deciding where to oviposit. If moisture attracts weevils to plants, then it would be worthwhile to investigate the effect of cultivars that produce higher biomass

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in terms of canopy cover and dead leaf material around the mat and higher mat density caused by higher suckering ability on weevil occurrence. This is true for Kayinja, and may be a reason why Abera (1998) found higher oviposition on this resistant cultivar. These factors could lead to a favourable microclimate (especially under the hot tropical sun) for weevils and may have implications for the control of banana weevil.

Antibiosis is no doubt the most important resistance mechanism in banana weevil resistance. This study has shown that resistant cultivars, especially Kayinja, Yangambi-km5 and FHIA03, have antibiotic effects on the development and survival of the banana weevil. Using high performance liquid chromatography, active compounds related to banana weevil resistance were observed, but these were mostly restricted to resistant cultivars with the B genome. A preliminary bioassay confirmed that the active components affecting weevil are polar in nature and it is recommended that work should continue in this aspect to identify, isolate and test the best active components for use directly as biological insecticides, or biochemical markers for resistance screening in a breeding programme. The full implications of these findings must therefore await further study.

In conclusion, banana weevil resistance is a complex trait, involving several factors operating in tandem. Possibly this is the reason for the inconsistent results observed from different studies. While some factors like corm hardness are important in some cultivars, other factors like secondary metabolites are important in others. This is further complicated by other factors operating in smaller percentages of clones (*e.g.* sap/resin production, suckering, and corm size). Most of these factors and their respective genes are responsible for resistance more so on the B genome rather than the A genome and with a pronounced dosage effect at higher ploidy levels. Antibiosis is the most important resistance mechanism to banana weevil in Ugandan *Musa* germplasm. Total inner damage is the most informative damage index since it takes into consideration penetration into the central cylinder where water and mineral uptake can be affected. It has a high genetic heritability and selecting for it in a breeding programme would lead to good selection success. Overall the factors responsible for antibiotic resistance in banana include corm hardness, dry matter content, resin/sap production and size of the corm and to a smaller extent suckering ability, the latter three of which are more important within the local EAHBs.

Although banana weevil resistance is a complex trait, some progress can be made through selections and the EAHBs such as Mbwazirume and Nakeytengu, which are already very popular cultivars selected and distributed widely over the decades of peasant cultivation, can be recommended. Better progress can be made through introgression with some of the exotic cultivars *e.g.* Yangambi-km5 and FHIA03 currently grown, and incorporate these in the ongoing breeding programme using conventional methods. One of the objectives at the beginning of this study was to obtain a phenotypic marker to be used for rapid screening of large populations against banana weevils and to avoid the tedious, long and expensive process of scoring damage at harvest. Unfortunately no such maker has been found and it is hoped that the search can only be aided with the use of recent advances in molecular markers. By using molecular markers, loci of quantitative traits (QTL's) can be found that are closely linked to the genes responsible for the trait. This can be of great help for traits like banana weevil resistance, which seems to be polygenic and whose expressions are complicated. QTL analysis will offer great hope for improving the efficiency of conventional banana breeding by carrying out selection, not directly on the trait of interest, but on molecular markers linked to that trait.

SUMMARY

Banana is an important subsistence crop in many tropical regions of the world. In the East African Great Lakes region it constitutes a staple food for more than 17 million people. Among many production constraints, banana weevil (*Cosmopolites sordidus*), is the most serious pest to the crop. The tunnels caused by the boring larvae interfere with water and mineral uptake, and provide entry for fungi and bacteria. Most importantly this weakens the corm, leading to toppling of plants even in slight winds. Host plant resistance is considered the basis of any successful integrated pest management plan, if the banana weevil problem is to be solved by the resource poor farmers.

The screening trial of 45 Ugandan *Musa* germplasm accessions revealed that the plantain subgroup (AAB) was most susceptible to banana weevil followed by East African highland banana clones. The exotic bananas, especially Kayinja, Bluggoe (ABB), Kisubi and Ndiizi (AB) were resistant to banana weevil. Plantain derived tetraploid hybrids of the wild banana Calcutta-4 were also susceptible, indicating dosage effect of the susceptible gene. Mbwazirume, Tereza and Nakyetengu have been found to be relatively resistant local land races and they are recommended as possible resistant selections. Total inner damage was found to be the best criteria for screening, and selecting for weevil resistance, since it scored the highest heritability and was highly correlated with all other weevil damage indices.

Significant phenotypic and genotypic correlations were found between corm hardness, dry matter content, sap/resin production, suckering ability and corm size and banana weevil damage. These were therefore considered important mechanisms of resistance in *Musa* and this indicated that banana weevil resistance is a complex polygenic trait.

In agreement with the literature studied, antixenosis was not found to be important as a resistance mechanism in *Musa*. However, results from various no-choice experiments on hatchability and development revealed significant differences. The previously observed resistance cultivars Kayinja, Yangambi-km5 and FHIA03, unlike the more susceptible plantains and EAHBs, significantly increased developmental time and in some cases caused mortality of immature weevil stages.

Preliminary studies on the influence of secondary metabolites were undertaken. The results showed the presence of two or three compounds indicated by peaks on HPLC chromatograms of methanol extracts of corms from resistant cultivars (*e.g.* Kayinja and FHIA03) that were not present in susceptible cultivars (e.g. Atwalira and Gonja). These substances were also not present in some resistant cultivars like Yangambi-km5 and Cavendish, both of the AAA genome group. This was yet another indication that resistance is complex and these different factors are important in different groups of cultivars.

Key words: banana, clones, *Cosmopolites sordidus*, genetic correlations, heritability, host-plant, *Musa*, pest, plantain, resistance, weevil

OPSOMMING

Piesangs (*Musa*) is 'n belangrike onderhoudgewas in heelwat tropiese streke van die wêreld. In die Oos-Afrika Groot Mere area is dit die stapel voedsel van meer as 17 miljoen mense. Piesang snuitkewers (*Cosmopolites sordidus)* die ernstigste plaag op piesangs, is een van 'n aantal produksie beperkings wat bestaan. Die tonnels wat daartoe lei word deur borende larwes benadeel water en mineraal opname en gee ingang aan fungi en bakterië. Die grootste probleem is dat die ondergrondse stam van die plant verswak word, wat veroorsaak dat die plant omval, selfs as 'n ligte wind waai. Gasheer plant weerstand word gesien as die basis van enige geïntegreerde plaagbestuursplan indien die piesang snuitkewer probleem opgelos moet word deur hulpbron arm boere.

Die evaluasie proef van 45 Ugandese *Musa* kiemplasma lyne het aangetoon dat die kook piesang subgroep (AAB), die mees vatbaar was, gevolg deur Oos Afrika hoogland piesang klone. Eksotiese piesangs, veral Kayinja, Bluggoe (AAB), Kisubi en Ndiizi (AB) was weerstandbiedend teen piesang snuitkewer. Kook piesang afgeleide tetraploïede basters van die wilde piesang, Calcutta-4, was ook vatbaar, wat aangetoon het dat daar 'n dosis effek is van die vatbare geen. Mbazirume, Tereza en Nakyetengu is aangetoon as redelike weerstandbiedende plaaslike landrasse en is aanbeveel as moontlike bronne van weerstand. Totale binne-skade is aangetoon as die beste kriterium vir evaluasie en seleksie van snuitkewerweerstand, omdat dit die hoogste oorerflikheid getoon het en die hoogste gekorreleer was met ander snuitkewer skade metings.

Betekenisvolle fenotipiese en genotipiese korrelasies is vir ondergrondse stam hardheid, droë materiaal opbrengs, sap/gom produksie, suier produksie vermoë en ondergrondse stam grootte en piesang snuitkewer skade gevind. Dit was dus die eienskappe wat as aanduiers van belangrike meganismes van weerstand in *Musa* gesien is. Piesang snuitkewer weerstand is aangetoon as 'n komplekse poligeniese eienskap.

Antixenose is nie aangedui as 'n weerstandsmeganisme in *Musa* nie. Dit was in ooreenstemming met werk van ander navorsers. Resultate van 'n aantal nie-keuse proewe vir eier uitbroeiing en ontwikkeling het betekenisvolle verskille aangetoon. In vorig geïdentifiseerde weerstandbiedende cultivars, naamlik Kayinja, Yangambi-km5, en FHIA03, het snuitkewers 'n betekenisvolle langer ontwikkelingstyd getoon, en in sommige gevalle was

daar mortaliteit van onvolwasse snuitkewer fases. Dit was in teenstelling met meer vatbare kook piesangs en Oos Afrika hoogland piesangs.

Voorlopige studies oor die invloed van sekondêre metaboliete is onderneem. Die resultate het die teenwoordigheid van twee of drie stowwe aangetoon by wyse van pieke op die HPLC chromatogram van metanol ekstrakte van ondergrondse stamme van weerstandbiedende cultivars (bv. Kayinja en FHIA03), wat nie teenwoordig was in vatbare cultivars nie (bv. Atwalira en Gonja). Hierdie stowwe was ook nie teenwoordig in sekere weerstandbiedende cultivars soos Yangambi-km5 en Cavendish, beide AAA genoom groep. Dit was nog 'n aanduiding dat weerstand'n komplekse eienskap is en dat verskillende faktore belangrik is in verskillende groepe cultivars.

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