CHARACTERIZATION OF RUSSIAN WHEAT APHID, *Diuraphis noxia*, (HOMOPTERA: APHIDIDAE) POPULATIONS IN KENYA

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A Thesis submitted to the Graduate School in partial fulfillment of the requirements for the Degree Master of Science in Crop Protection

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DECLARATION AND RECOMMENDATION

Declaration

This thesis is my original work and has not been previously presented to this or any other university for the award of any degree.

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This thesis has been submitted for examination with our approval as University supervisors.

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DEDICATION

This thesis is dedicated to my father, Ngenya Atsiambo who taught me to work hard, my mother Phoebe Ngenya who taught me to love, my siblings who taught me to share, my Uncle Simon Ambani who taught me to believe in myself, and to God who enabled me to achieve this dream.

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ABSTRACT

The Russian wheat aphid (RWA) *Diuraphis noxia* (Kurdjumov) is a serious pest of wheat in Kenya. Development and use of RWA resistant wheat (*Triticum aestivum* L.) varieties, has been constrained by variations in the resident RWA populations and evolution of virulent biotypes. To fully exploit host plant resistance (HPR) in management of RWA, resident populations of RWA were evaluated for biotypes in order to develop and deploy cultivars that exhibit cross biotype resistance. Three experiments were conducted in a greenhouse at KARI-Njoro to characterize population dynamics, host choice and virulence of RWA populations from the endemic areas (Eldoret, Mau Narok, Njoro and Egerton) in Kenya. The first experiment sought to determine variations in population characteristics and survivorship of RWA populations on KRWA9 which contains an unknown *Dn* gene and a susceptible host, Kenya Kwale (Kwale). A factorial experiment was set up in randomized complete block design (RCBD) replicated eleven times. A single, day old nymph was placed on a new fully open leaf in a 0.5mm diameter clear plastic straw leaf cage and observed daily. There was variation in aphid lifespan, reproductive longevity and aphid fecundity between populations. The second experiment was to determine variation in RWA preference for four host genotypes; AUS7 containing *Dn4* gene, AUS9 containing *Dn7* gene, KRWA9 which contains an unknown *Dn* gene and susceptible Kwale. This was a factorial experiment in RCBD replicated three times. Results indicate that Kwale, a susceptible variety was the preferred host and Eldoret population had significantly more numbers finding a host as compared to the other populations. The third experiment was a factorial experiment in RCBD replicated three times to determine virulence of the RWA aphids at seedling stage in the greenhouse. Five adult RWA aphids from each RWA location were used to infest four host genotypes; AUS7, AUS9, KRWA9 and Kwale, for 28 days. Results show that Egerton and Njoro populations were more virulent than populations selected from other areas indicating that at least two RWA biotypes exist in Kenya.

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LIST OF ABBREVIATIONS

1. ANOVA Analysis of Variance.
2. FAO Food and Agriculture Organization
3. IPM Integrated Pest Management.
4. LSD Least Significant Difference.
5. RWA Russian Wheat Aphid.
6. S.E. Standard Error of the Differences of the means.

CHAPTER ONE

INTRODUCTION

1.1 Background Information

Wheat, (*Triticum aestivum* L.), is the second most important cereal crop in Kenya. The estimated 300,000 metric tons produced annually on 150,000 hectares of land, however meets only 30% of the domestic requirement (FAO, 2005). The rapidly increasing population and changing lifestyles implies more wheat has to be produced. Since the medium to high potential agricultural land for wheat production in Kenya is limited, increased yield will be achieved only through intensifying production per unit area. The increase in yield per unit area is however constrained by pests and diseases.

Cereal aphids are some of the major pests of wheat in Kenya: They include *Schizaphis graminum, Rhopalosiphum padi, Rhopalosiphum maydis, Sitobian avenae, Metapolophium dirhodum* and *Diuraphis noxia* (Wanjama, 1990; Nyaanga *et al*., 2006). The Russian wheat aphid, (*Diuraphis noxia* Kurdjumov.) first identified in farmers fields in 1995 (KARI, 1998) is currently the most important aphid species limiting wheat production. The pest causes up to 90% yield loss (Kinyua *et al*., 2002; Macharia *et al*., 2004; Maling'a, 2007). The aphid feeds by pushing its stylet into the phloem vessels, before proceeding to suck the sap. At the same time the pest injects toxic saliva into the plant tissues resulting in leaf chlorosis, leaf folding, leaf rolling, reduced plant height (stunting), reduced shoot weight, and reduced photosynthetic area (Girma *et al*., 1993). The damage to the leaf mesophyll cells and vascular bundles during RWA feeding causes apoplastic and symplastic isolation of the xylem and phloem tissues which results in transport ceasure, wilting and eventual death of the plant occur (Saheed, 2007; Zaayman, 2007). The tightly rolled flag leaf also trap the reproductive parts hence interfering with pollination, fertilization and grain filling (Sandstrom *et al*., 2000; Saheed, 2007). Traditionally insecticides such as Oxydementon-methyl, Imidachlorprid and Thiamethoxam are used to control

RWA. The financial and environmental costs of using these insecticides are however too high for most farmers.

Host plant resistance is one of the most important alternative methods for the management of the Russian wheat aphid (Tolmay *et al*., 2000). In Kenya, the development of RWA resistant varieties has been hampered by concerns of possible existence of biotypes (Kiplagat, 2005; Malinga, 2007), insects within a species that vary in biological characters such as virulence, adaptation for survival and development on a particular host or by host preference for feeding, oviposition or both (Diehl and Bush, 1984; Puterka *et al.,* 1992; Haley *et al*., 2004). Kiplagat, (2005) found that the resistant line halt succumbed to RWA population from Nakuru while remaining resistant to populations from Eldoret. Subsequent work also raised concerns of existence of biotypes when Malinga (2007) found limited genetic variations among resident populations of RWA collected from Timau and Njoro. Evolution of virulent Russian wheat aphid biotypes hinder the sustainability of resistant wheat varieties and therefore resident RWA populations need to be characterized and described to establish the status of biotypes so that control can be rationalised.

1.2 Statement of the Problem

Currently Kenya produces only about 30% of its annual wheat requirement as farmers continuously realize sub-optimal wheat yields because of RWA infestation. While development and utilization of HPR for RWA management is important for wheat production, preliminary information show presence of RWA biotypes. The limited characterization of the biotypes however jeopardize utilization of HPR in the control of RWA

1.3 Justification

Wheat is the second most important cereal crop in Kenya. Its production is however constrained by the Russian wheat aphid which causes up to 90% yield loss. Management of the aphid through host plant resistance is cheaper and ecologically friendly. When resistant cultivars are grown widely, selection pressure is imposed on insect populations. The insect population respond with

development of genotypes having virulence to overcome the host plant resistance. The virulent insect genotypes with superior fitness replace the previously avirulent insect populations resulting in a breakdown of resistance and ineffective control of pest population. Preliminary studies show that biotypes of RWA exist in Kenya. The resident RWA populations in Kenya need to be characterized to determine their fitness and virulence on selected lines of wheat with resistance to the aphid.

The information generated from this research will lay the basis for breeding strategies to use in developing resistant varieties of wheat. It will also help in determining the best gene deployment strategy to manage the aphid in case there are RWA biotypes with differential fitness and virulence.

1.4 Objectives

1.4.1 General Objective

To contribute to increased wheat yield through effective management of the RWA in Kenya.

1.4.2 Specific Objectives

1. To determine resident RWA populations' host preference and population growth on selected host genotypes of wheat
2. To determine virulence of RWA populations on selected wheat genotypes based on damage level in a no-choice test.

1.5 Hypotheses

1. There are no differences in RWA population preference and population growth on selected wheat genotypes.
2. There are no differences in the virulence of RWA populations on selected wheat genotypes.

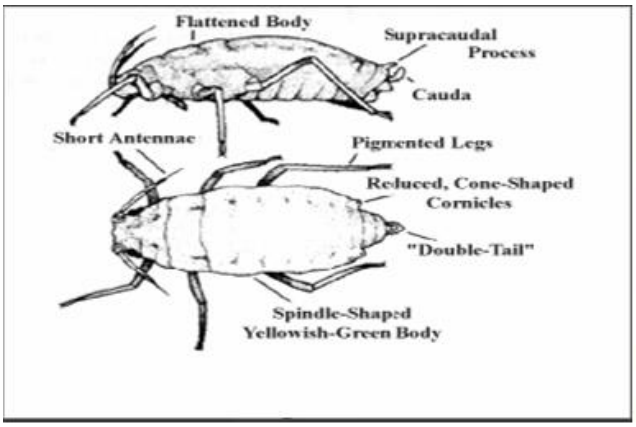
CHAPTER TWO

LITERATURE REVIEW

2.1 Russian wheat aphid origin, morphology and life history

The Russian wheat aphid, *Diuraphis noxia* Kurdjumov, is a species of the genus *Diuraphis*, family Aphididae, superfamily Aphidoidea, superorder Homoptera, and order Hemiptera (Black and Eastop, 2000). The Russian wheat aphid is indigenous to the wheat growing regions of central Asia, Southern Russia, Iran, Afghanistan and countries bordering the Mediterranean (Liu *et al.*, 2010). It is believed that the aphid spread from its native ranges to South Africa and on to Mexico and the greater Americas. The aphid has since spread to most of the wheat producing regions of the world except Australia (Basky, 2003).

The Russian wheat aphid is a small pale yellow to light green aphid dusted with white wax powder. It has an elongated, spindle shaped body and grows to up to 2 mm long. It has short antennae with rounded very short, nearly invisible cornicles. The feature that easily distinguishes RWA from other cereal aphids is the presence of an appendage (Supracaudal process) above the cauda, giving the aphid the appearance of having two tails (Black and Eastop, 2000; Michaud and Sloderbeck, 2005; Puterka *et al.*, 2010).



Source (Peairs et al.,2006)

Figure 1. Apterous Russian wheat aphid identification characteristics and an adult apterous female

2.2. Russian wheat aphid biology

The aphids feed on the plant until the plant dies down as it matures or in response to heavy aphid feeding. In such instances an increased proportion of the immature aphids (nymphs), in response to unfavorable conditions such as food shortage or overcrowding, develop wings that look like shoulder pads on third and fourth instar nymphs. These grow into alate female adults which fly away to colonize new wheat fields (Gibson and Rice, 1989; Nyaanga, 2002).

The alatae (winged) female adults differ in biology and appearance from their apterous (wingless) sisters. They give rise to few young ones because most of their stored food reserve is used during flight (Dagg, 2002; Michaud and Sloderbeck, 2005). They may feed for several days on the plant where they were born, but they do not begin reproducing until they fly away and find a fresh suitable host. They take to flight in response to the blue ultraviolet light from the sky and fly upwards (Gibson and Rice, 1989). They are carried on wind currents for long distances. Their function is to seek a suitable host plant and initiate a new colony (Black and Eastop, 2000). When descending from the sky, the Russian wheat aphid is attracted to the orange-yellow-green light reflected from leaves of plants. The size, shape and contrast of plants against its background affect its attractiveness to the alatae (Gibson and Rice, 1989).

Infestations often begin along field borders where the contrast between young plants and bare soil is greatest (Michaud and Sloderbeck, 2005). The alate (winged) aphids have well developed wing muscles and fat bodies that store energy for flight, they have smaller reproductive organs and are thus less fecund than their apterous (wingless) (Dagg, 2002). The daughters born to the colonizing alate aphids invariably develop into wingless adults which give birth to more daughters thus accelerating colony growth in the second generation (Le Trionnaire *et al.*, 2008).

The Russian wheat aphid feeds on the adaxial (upper) leaf surface and modifies the host plant to suit its own nutritional, developmental and colonization requirements (Cabrera *et al.*, 1995; Moran and Thompson, 2001). Longitudinal leaf rolling allows high density colonies to form in a protected

location. Rolled leaves also create a favorable microclimate for the aphid colony, buffering it from temperature extremes and reducing the risk of desiccation when relative humidity is low and dislodging in disturbances (Shea *et al.*, 2000; Michaud and Sloderbeck, 2005).

In addition, many larger aphid predators and parasitoids that attack Russian wheat aphids are less likely to encounter them in rolled leaves or less inclined to forage in such close quarters (Clark and Messina, 1998). Aphids hidden in rolled leaves, leaf whorls and leaf sheaths are better protected from contact insecticides, consequently, only systemic insecticides and aphicides are superior for Russian wheat aphid control (Gray *et al.*, 1996; Michaud and Sloderbeck, 2005)

2.3. Feeding and symptoms of damage

The Russian wheat aphid feeds in groups, developing and reproducing at higher rates and reducing their individual risk of attack by natural enemies (Qureshi and Michaud, 2005). Russian wheat aphid like many other hemipterans feed on phloem sieve elements while delicately keeping these cells alive and their sieve plate pores open by preventing coagulation of the phloem proteins (Tjallingii, 2006).

The aphid pushes its stylet into the plant tissue while secreting gelling saliva that forms a sheath around the stylet until the stylet reaches the sieve tube element when the aphid begins to secrete watery saliva that prevents protein coagulation both in the sieve tube and in the aphid stylet (Douglas, 2006; Tjallingii, 2006). The aphid sucks phloem sap while at the same time injecting toxic saliva into the plant tissues. The saliva causes galling, leaf deformation and rolling. The leaf rolling traps reproductive parts in tightly rolled leaves thereby limiting pollination and fertilization. The toxic saliva also affects vascular tissues (Sandstrom *et al.*, 2000; Saheed, 2007)

The leaves of susceptible wheat infested by Russian wheat aphid develop long whitish, purplish or yellowish streaks. The tillers of infested wheat may develop a purplish color especially in cold weather. Heavily infested plants are

stunted and some may appear prostrate, flattened or onion like (Shea *et al.*, 2000). The trapped heads are twisted or distorted and have a bleached appearance. Heads often have a “fish hook” shape caused by awns trapped by a tightly curled flag leaf (Michaud and Sloderbeck, 2005). At this time, Russian wheat aphids are found feeding on the stem within the flag leaf sheath or on developing kernels, causing poor grain filling (Michaud and Sloderbeck, 2005; Saheed *et al.*, 2006).

2.4. Lifecycle, reproduction and development

Aphids are characterized by their ability to reproduce either sexually or asexually (parthenogenesis) and ability to give birth to live young nymphs a phenomenon called vivipary (Dixon, 1977; Moran, 1992; Le Trionnaire *et el*, 2008). A single RWA female can produce 40 to 50 nymphs during her lifetime of 40 days. The nymphs take between 7 and 10 days to mature to adults and begin reproduction (Aalbersberg *et al.*, 1987). The aphid has holocyclic lifecyle (Figure 2) in severe temperate climates like Russia where winters are severe, RWA reproduces by series of parthenogenetic (non sexual) female viviparae generations from spring to fall under warm temperatures and a sexual generation in autumn. In these temperate climates, RWA eggs are cold tolerant and this is the overwintering stage. In the tropics and mild temperate climates where winters are not severe, the aphid has an anholocyclic lifecycle (Figure 3) reproduction where there is permanent parthenogenesis (Puterka *et al.*, 2010).

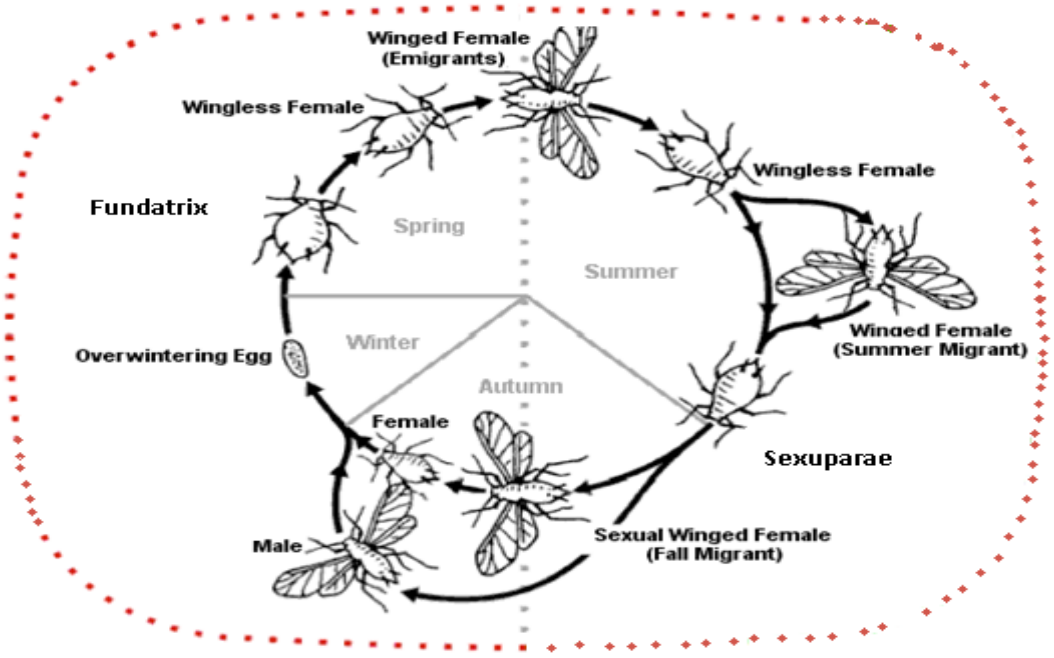


Figure 2. Holocyclic Lifecycle of the Russian wheat aphid *Diuraphis noxia* (Kurdjumov)

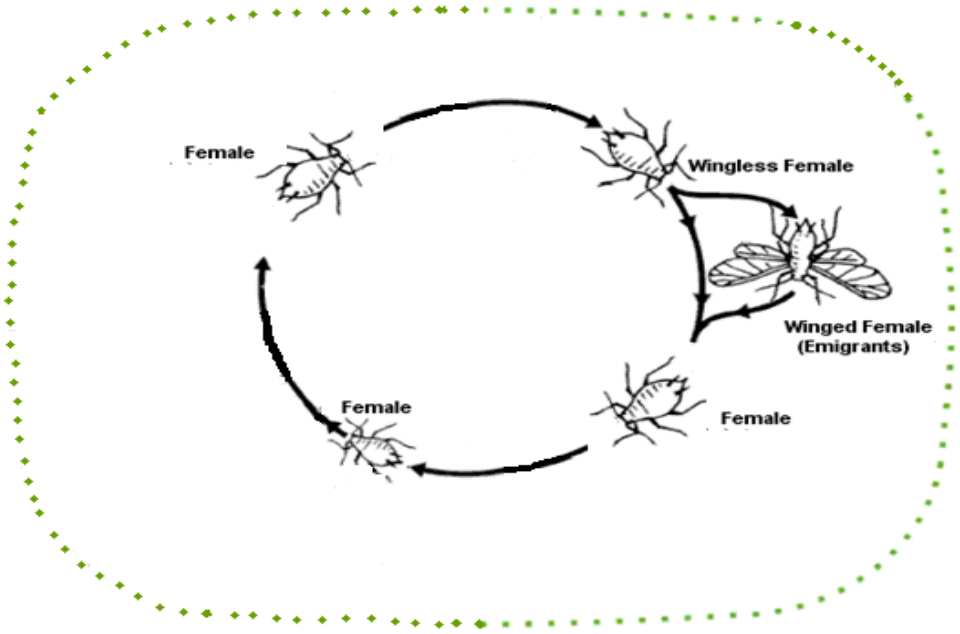


Figure 3. Anholocyclic Lifecycle of the Russian wheat aphid *Diuraphis noxia* (Kurdjumov)

The environment plays an important role in reproduction and development of the Russian wheat aphid. Environmental factors such as temperature, humidity and light intensity usually influence rate response of activities such as feeding, dispersal, reproduction and development. Temperature has the greatest effect on aphid reproduction and development because rate of development increases with increase in temperature within limits (Aalbersberg *et al*., 1987; Michels and Behle, 1988)

The Russian wheat aphid usually undergoes sexual or asexual reproduction depending on the environmental conditions (Dixon, 1977; Moran, 1992; Le Trionnaire *et al,* 2008). All adult aphids in warm climates (tropics) are female. Female aphids give birth to live daughters which are carrying embryonic granddaughters. This rapid asexual reproduction is the key to the explosive population growth achieved by the RWA and many other aphid species (Dixon 1977; Dagg, 2002; Clua *et al,* 2004).

Asexual females in response to extremely low temperatures and short day length (16D:8L) produce a sexual producing female known as a sexupara. Sexuparae then asexually produce both sexual females and males. Sexuals mate and lay overwintering eggs. This genetic recombination is an important source of s genetic variation within an aphid population. The hatched females later undergo parthenogenetic reproduction and found new clones (Moran, 1992).

2.5 Russian wheat aphid management strategies

2.5.1 Chemical control

The control of Russian wheat aphid in Kenya is currently through the use of chemicals (aphicides) to kill aphids already established on the crop. Insecticides with systemic mode of action such as Cruiser (Thiamethoxam), Metasystox (Oxymenton-methyl) and Gaucho (Imidachloroprid) are currently the most effective aphicides in the management of Russian wheat aphid (Macharia *et al*., 2004). Contact insecticides cannot reach Russian wheat aphid which feeds inside rolled up leaves, deep in leaf whorls and the leaf sheaths of the infested plants (Qureshi and Michaud, 2005).

The use of chemicals for Russian wheat aphid control sometimes harms beneficial insects that naturally regulate the pest population (Rauscher, 2001; Nyaanga, 2008)

2.5.2 Biological control

The interaction between insects and their natural enemies is an essential ecological process that contributes to natural regulation of an insect pest population. Several aphidophagous ladybird species that predate on cereal aphids have been documented. The predators and parasitoids known to attack cereal aphids includes; Coleoptera: *Adonia variegate, Chilomenes* spp., Hymenoptera: *Aphidius* spp and *Aphelinus* spp., Diptera: syrphidae (hover flies), Arachnoidea (spiders) and Neuroptera (lacewings) (Brewer *et al*., 2005). Nyaanga, (2008) however found out that the efficacy of biological control for RWA is affected by various cultural practices including chemical application. Also, peak populations of predators' and parasitoids often occur after peak infestation by the aphid, hence resulting in ineffective control of the RWA (Adisu *et al.,* 2003). It is therefore imperative that biological control be supported by other control measures in an integrated management of RWA.

2.5.3 Cultural control

Cultural control involves the use of production techniques that result in a crop environment that is less favorable for the pest or more favorable to the natural enemies of the pest (Dent, 1991). Farming practices that result in healthier and more vigorous crop help to minimize damage by aphids and other pests (Tilman *et al*., 2002). When seasonal variation in aphid abundance is known the variation of planting date can be used to manage the pest damage on wheat from cereal aphids. In Kenya, planting late in the wheat season increases infestation whereas wheat planted at the onset of rains is known to escape Russian wheat aphid infestation because heavy rains are unfavorable for aphid establishment (Maling'a, personal communication)

2.5.4 Host plant resistance

Insect pests and their crop hosts have coexisted for a long time. Each plant species has self defense traits ranging from morphological features to plant biochemicals that affect the behavior and physiology of potential insect pests (Rauscher, 2001).

Definitions of an insect resistant plant are many and varied. Plant resistance is defined as the consequences of heritable plant qualities that result in a plant being relatively less damaged than a plant without these qualities (Painter, 1951). An insect resistant cultivar is one which when confronted by the pest results in relatively less damage (Dent, 1991). Resistance of plants to insects is a relative measure based on comparison with susceptible plant (Painter, 1951; Dent, 1991). Insect resistant crop varieties alter relations with the pest and suppress insect pest abundance or elevate the damage threshold of the plant.

How the relationship between a plant and an insect pest is affected depends on a set of mechanism of resistance that includes antibiosis, non-preference or tolerance (Painter, 1951; Du Toit, 1987). Non-preference has recently been replaced by the term antixenosis, which is the resistance mechanism a plant uses to deter colonization by an insect pest. Insect pests orientate towards a host plant for food, oviposition and shelter, but some plant characteristics may make the plant unacceptable to the pest (Painter, 1951; Dent, 1991; Rauscher, 2001). Antibiosis is a mechanism by which a colonized host plant is resistant because it has adverse effect on the pest reproduction, development and survival. The antibiotic effects may result in a decline in an insect's size or weight due to increased restlessness or poor food assimilation affecting an insect's survival ability (Dent, 1991; Rauscher, 2001; Kessler and Baldwin, 2002). Tolerance however is the extent to which plants can support an insect infestation without loss in vigor and reduction in crop yield. A vigorous crop is tolerant if it can compensate for pest infestation by higher yield compared to a crop that is susceptible (Rosenthal and Kotanen, 1994; Kessler and Baldwin, 2002)

Breeding efforts to develop Russian wheat aphid resistant varieties started in South Africa shortly after the introduction of RWA in 1978. Three genes designated *Dn1, Dn2* and *Dn5* were identified in wheat *T. aestivum* L. which led to the first RWA resistant cultivar (Tugela*Dn*). Tolmay *et al.*, (2007) reported that by 2006, 26 resistant cultivars had been released in South Africa. Nine RWA resistance genes for wheat have been characterized by South African and United States of America researchers. *Dn1, Dn2, Dn4, Dn5, Dn6, Dn8* and *Dn9* which are single dorminant genes originated from *T aestivum*. The recessive *Dn3* gene originated from *T tauschii* whereas the dorminant gene *Dn7* resulted from an intergeneric transfer from rye to wheat (Marais *et al*., 1994)

2.6 The biotype concept and overcoming host resistance

Russian wheat aphid biotypes are distinguished from each other based on on ability to overcome host resistance, aphid fecundity and ability to cause differential damage in host differentials (Puterka et al., 1992; Burd et al, 2006: Jyoti et al., 2006: Randolf *et al.*, 2008). Biotypes of other organisms are designated for a variety of reasons including herbicide resistance for weedy plants and overcoming plant resistance mechanisms, competitive ability, virus transmission ability, and insecticide resistance for insect pests.

Traditionally, the term insect biotype refers to insects that closely resemble one another morphologically, but differ from each other on the basis of host preference and survival under adversity (Diehl and Bush, 1984). They are individuals or populations of an insect pest species that show differences in phenotypic expression of virulence (Dent, 1991). This shows that insects that have the same genes for virulence may differ in their adaptability to hosts with different genes for resistance (Randolf *et al.*, 2008). Many insect species that have evolved biotypes are insect pests of grain crops such as wheat, barley, sorghum and rice, and they are specifically described by their ability to injure crops with host plant resistance genes (Puterka *et al.*, 1992, Porter et al. 1997) In aphids and other pests that are largely managed by host plant resistance, this

ability to injure or survive favorably on previously resistant plants is the generally accepted criterion for biotype designation.

Biotypes of insects can develop due to random mutations, existing variability within the pest population, sexual recombination or other unknown reasons (Rauscher, 2001). Aphid clones (asexual lineages) randomly mutate and though this mutations cause minor variation in insect genotype, some of this variation is transmissible and adaptive (Lushai and Loxdale, 2002; Loxdale, 2008). The enormous potential for asexual reproduction in aphids magnifies the minor variations and biotype differentiation. Though genetic recombination through sexual reproduction contributes to genetic variability in a pest population, this method of creating genetic variability within an aphid population in tropical climates is insignificant. Aphids in the tropics undergo obligate parthenogenesis and therefore ideally there would be no genetic variability in aphid populations in these climates (Wilson and Sunnucks, 2006).

A RWA population can contain biotypes that have the ability to damage cultivars or varieties that have resistance genes (Table 1). The occurrence of RWA biotypes can have a serious impact on management of Russian wheat aphid using host plant resistance and biological control. Failure to recognize distinct biotypes in aphid populations often lead to ineffective control measures being used to manage the aphid. The genes used in a resistant variety may be broken down by some biotypes and sometimes the biological agents introduced to control the aphid may not have preference for some of the aphid biotypes thus leading to ineffective control of the aphid (El Bouhssini *et al*., 2001).

Biotypes were first reported in RWA populations from the former USSR, Europe and the Middle East in 1989. Russian wheat aphid from Syria and Kyrgiz were found to be virulent to *Dn*4 resistance gene in wheat (Puterka *et al*., 1992; Basky 2006). Haley *et al*, (2004) identified a virulent biotype in Colorado that could acutely damage wheat with any one of the eight of nine *Diuraphis noxia* (*Dn*) resistance genes with the exception of *Dn7* and designated this biotype as RWA2. The other Russian wheat aphid biotypes, RWA3, RWA4, and RWA5

have the ability to differentially damage wheat with *Dn*1 to *Dn*9 resistance genes in wheat (Burd *et al.,* 2006).

Table 1. Russian wheat aphid resistance genes and biotype interactions in wheat in the USA

	Russian wheat aphid biotype				
	RWA1	**RWA2**	**RWA3**	**RWA4**	**RWA5**
Gene	**Reaction to biotype**				
Dn 1	S	S	S	S	S
Dn 2	R	S	S	S	S
Dn 3	R	S	S	S	S
Dn 4	R	S	S	R	R
Dn 5	R	S	S	S	R
Dn 6	R	S	S	S	R
Dn 7	R	R	S	R	R
Dn 8	S	S	S	S	S
Dn 9	S	S	S	S	S

R and S indicate Resistant and Susceptible reactions respectively (Burd *et al.,* 2006)

2.7 Russian wheat aphid biotype situation in Kenya

The origin of new RWA biotypes in tropical populations remains critically undetermined. The threat of new RWA biotypes to wheat production is not limited to the USA or South Africa (Tolmay et al., 2007). In Kenya, Kiplagat,(2005) reported that Mbuni, Kongoni and Halt were susceptible to Russian wheat aphids isolates from the four locations(Nakuru, Eldoret, Laikipia and Narok) based on chlorosis and leaf rolling whereas the line PI 294994 was found to be highly resistant to Russian wheat aphid isolates from the four the locations. He concluded that it was unlikely that there were different biotypes of the aphid in the 4 wheat growing areas. The susceptibility of Halt a resistant cultivar with Dn 4 resistance gene from the USA however indicated that there was a biotype different from the wild type in the USA that could be controlled using Dn4 and which had been designated as RWA 1. Malinga (2007) conducted a study to determine the biotype status of Kenyan RWA populations and found limited genotypic variations among Kenyan RWA populations. These results just

like those of Puterka *et al*. (1992) and Weng *et al*. (2007) found that there were genetic variations among RWA populations from different locations of the world. Liu *et al*. (2010) went further in their study and determined patterns of genetic divergence among RWA populations from around the world and clustered RWA populations into three clusters based on their relations to each other. All these studies showed little evidence of any association between variation in aphid genotype and phenotypic expression of the biotype. Traditionally, biotypes have been defined based on their effects on resistant plants, not genetic divergence among aphid populations. From Kiplagat (2005) and Malinga (2007), the conclusions were that there was a possibility thatthere were more than one RWA biotype in Kenya and thus the need to conduct studies to determine the biotype status of Russian wheat aphid in Kenya. RWA biotypes that are virulent to known resistance genes puts into jeopardy deployment of such genes in any breeding program (Kiplagat, 2005). The origins of biotypes in Kenya could be due to the existence of variability within the original migrant populations of the Russian wheat aphids into Kenya or due to random changes that could have occurred within the aphid population due to extensive use of aphicides to manage wheat aphids in Kenya (Maling'a, 2007).

Biotype diversity among the insects can be detected using simple estimates of population growth parameters and virulence to host plant (Edwards, 2001). The determination of biotypic diversity and characterization of the biotypes in terms of virulence and population dynamics is important for integrated management of Russian wheat aphid and for breeding effective resistant varieties.

CHAPTER THREE

MATERIALS AND METHODS

3.1 Site Description

The study was conducted in the greenhouse at Kenya Agricultural Research Institute, Njoro,(0°20'S 35°56'E), located in the lower highlands (LH_3), at an altitude of 2166 meters above sea level. The temperatures ranged between 18–28°C during the period of the study, while the average annual rainfall is about 1,000 mm. The soils are deep, well drained, fertile *Vitric Mollic Andosols*. (Jaetzold and Schmidt, 1983)

3.2 Potting Media Preparation

The potting mixture was composed of mixture of forest soil, sand and manure ratio in the ratio 3:1:1. The potting mixture was steam autoclaved at 120^0C to eliminate pests and disease pathogens. The potting mixture was then amended with the equivalent of 50 kg DAP /ha.

3.3 Aphid Populations and Aphid Collection

Four aphid populations were collected from different areas (Table 2) within the country. The populations included; Egerton population, Eldoret population, Mau narok population and Njoro population.

The RWA were identified based on morphological descriptions using X10 magnifying glass (Black and Eastop, 2000; Puterka et al., 2010). The RWA were collected together with leaf sections of host and placed in Petri dishes having moistened blotting paper and transported to KARI, Njoro to be reared and maintained on susceptible Kenya Pasa.

Table 2. Russian wheat aphid populations used in the study

Sno	Population	Collection point	Altitude	Original host
1.	Egerton	Egerton University, Njoro, (0°22'S 35°56'E)	2265 masl	Rye grass
2.	Eldoret	Moi University, Chepkoilel, (0°34'N 35°18'E)	3085 masl	Bread wheat
3.	Mau Narok	Maasai Purko farm, Tipis, (0°36'S 36°00'E)	2829 masl	Bread wheat
4.	Njoro	KARI, Njoro (0°20'S 35°56'E)	2166 masl	Bread wheat

3.4 Inoculation and Aphid Rearing

Several seeds of the rearing plants Kenya Pasa (Pasa) were planted in a one litreL plastic pot and the pots placed in a water bath in an insect rearing box (Figure 3) to keep the emerging seedlings clean from aphid contamination in the greenhouse. The plants were watered regularly by replenishing water in the water bath after every three days so that the seedlings were not water stressed.

Figure 4. Insect rearing box

A single adult female RWA was settled in the leaf whorl of clean susceptible wheat seedlings of variety Pasa at growth stage 12 (Zadoks *et al.*, 1974) using a fine hair brush. The inoculated seedlings were then caged in ventilated plexiglas insect rearing boxes in the greenhouse under natural light conditions. The aphids were allowed to multiply freely to form a colony. The insect rearing boxes were designated

for specific populations and were kept a minimum 10m from each other to eliminate mixing of the populations. The aphid colony in an insect rearing box was named after the place where the founder aphid was collected from and designated as either Egerton, Njoro, Eldoret or Mau Narok populations.

3.5 Host Genotypes

Wheat genotypes used in the study were sourced from Kenya Agricultural Research Institute (KARI), Njoro. Four genotypes, Kenya Kwale (Kwale), KRWA9, AUS7 and AUS9 were use during the study. Kwale was released in 1975, and is a popular Kenyan variety grown in most wheat growing areas. It is however susceptible to Kenyan populations of RWA and was used as the susceptible control. KRWA9 on the other hand is an introduced line identified for resistance to the RWA populations in Kenya and is currently used in the crossing block. AUS7 and AUS9 are newly introduced lines identified for resistance to RWA in the USA with the later having global resistance.

3.6 Experiments

3.6.1 Determination of Russian wheat aphid populations' host preference and performance on selected wheat genotypes

Experimental design

The experiment was 4X4 factorial experiment arranged in randomized complete block design (RCBD) replicated three times. A single pot one litre in size containing all four test genotypes and four RWA populations and comprised a replicate. All three replicates assigned to a given population were held in one insect rearing box to prevent contamination

Wheat genotypes

The genotypes used included: Kwale, KRWA9, AUS7 and AUS9 obtained from KARI, Njoro.

Aphid populations

Aphid clones used included Eldoret population, Mau Narok population, Njoro population and Egerton University.

Infestation and experimental management

Two seeds of each genotype were planted randomly equidistant from each other on the periphery of a single plastic pot (1litre capacity). The pot was then caged with 1mm mesh cloth supported on wire supports to prevent infestation by RWA or other cereal aphids. After germination the seedlings were thinned to leave one of each genotype per pot. At the 2 leaf stage, 100, third and fourth instar nymphs from each population were released at the centre of each pot at 4.00 pm. Each pot was then covered with polyester mesh cloth (1mm) supported on wire supports.

Parameters measured

The number of aphids that settled on each wheat genotype was counted 24 hrs after infestation. The number of aphids on each wheat genotype served as an indicator of aphid clone preference/ acceptance of the wheat genotype as a suitable host for the aphid population.

3.6.2 Effect of selected wheat genotypes on population growth of Kenyan populations of RWA

Treatments

Aphid population and wheat genotype were factors in the experiment. Aphid population had three levels, Eldoret population, Mau Narok population, and Njoro population while wheat genotype had two levels, Kwale and KRWA9.

Experimental design

The experiment was a 2x3 factorial experiment in randomized complete block design (RCBD) with eleven replications.

Infestation and experimental management

Two seeds of Kwale and KRWA9 genotypes were planted in individual pots filled with an autoclaved mixture of forest soil to manure ratio of 3:1 and supplemented with DAP at the equivalent rate of 50 kg/Ha. Thirty three pots of Kwale and 33 pots of KRWA9 were planted and arranged in a randomized complete block design on a greenhouse bench.

After germination the seedlings were thinned to leave one seedling per pot. At the two leaf stage, the midsection of one leaf was enclosed inside a leaf cage made from 5mm diameter clear plastic straw cage measuring 3cm long. The straw leaf cage had earlier been ventilated with 20 holes made by piercing the straw using an insect pin. The leaf tip was then placed at one end of the cage and the cage moved towards the plant stem until the middle of the leaf was enclosed. Each plant leaf section was then infested with one adult RWA from a RWA population and both the ends of the cage plugged with a piece of cotton wool. After 12 hours, the cages were unplugged and the adult and young larviposited nymphs removed to leave only one nymph per cage. The nymphs of about the same age were caged on leaves of test plants.

The retained nymphs were observed on a daily basis for molting, reproduction and death of aphids. Aphids were moved to fresh leaves when the caged leaf section aged and started to turn yellow. Temperature was recorded daily for the entire duration of the experiment. Test plants were watered regularly throughout the duration of the study based on visual observation of the soil surface.

Parameters measured

The following data was collected:

i. Instar development time (days taken for a nymph to molt).
ii. Development time (days from birth to the date of first larviposition).
iii. Reproductive longevity(time taken from day of first reproduction to cessation of reproduction or death whichever occurred first)
iv. Total longevity (time from birth to death)
v. The number of nymphs produced daily.
vi. Total progeny (total number of nymphs born in a single aphids lifespan).

In order to determine how the host genotype influences a populations' rate of population increase, the intrinsic rate of population increase (r_m) for each aphid population on each wheat genotype was calculated using the method of Wyatt and White, (1977)

$$rm = \frac{0.738(\ln Md)}{d} \quad \text{.....Equation 1}$$

d is the development time from birth to first reproduction

M_d is the number of offspring that were produced in a time d.

Cohort generation time (T_c) for each population was calculated using the formula

$$Tc = \frac{4d}{3} \quad \text{.....Equation 2}$$

d is the development time from birth to first reproduction

3.6.3 Determining the virulence of Kenyan populations of Russian wheat aphid on selected wheat genotypes

Factors

Aphid populations used included Eldoret, Mau Narok, Egerton and Njoro. Wheat genotypes Kwale, KRWA9, AUS7 and AUS9 sourced from KARI, Njoro were used in the study

Experimental design

The experiment was a 4X5 factorial experiment laid out in a completely randomized design with three replications.

Infestation and experimental management

Two wheat seeds were planted in a sterilized mixture of soil and manure in the ratio 3:1 and amended with 50 kg/ha Diammonium phosphate DAP and 2g Copper Oxychloride/1L pot. Three seeds were planted per pot and later thinned to two seedlings per pot. Water was supplied regularly by standing pots in a water bath for two hours after every two days so that the seedlings were not water stressed. At growth stage12 (Zadoks *et al*., 1974) the test plants were inoculated with four apterous (wingless) Russian wheat aphid adults. Two

aphids were placed in the leaf whorl of each test plant using a fine hair brush. The infested pots were then be caged using ventilated polyester mesh supported on wires and the aphids left to multiply and feed on the test plants for 28 days. Temperatures range during the duration of the experiment was between 18–28°C

Parameters measured

Scoring for overall plant damage was done at 7 days, 14 days, 21 days and 28 days post inoculation, the damage to the test plants were qualitatively evaluated using a 1-9 scale as shown in Table 3 (Maling'a, 2007; Tolmay, 2007) Plant height was measured 28 days after infestation (DAI). The plants were then cut at the soil surface and weighed to determine fresh weight. The sampled plants were dried at 105^0C for 48hrs, and weighed to determine above ground biomass. Proportional height, fresh weight and dry weight was also determined using the formular

$$DWT = \left(\frac{D_c - D_t}{D_c}\right) * 100$$ **.....Equation 3**

DWT- Proportional reduction

D_c- Value measured on non infested control plant

D_t- Value measured on infested plant

Data Analysis

Analysis of variance (ANOVA) using Genstat the general linear model, Significant differences in treatment means were separated using Least significant difference (LSD) at α= 0.05 level of significance.

Table 3. Damage rating scale (1-9) used to characterize reaction types and classes to RWA on infested plants

Rating	Description of symptoms	Variety classification
1	Small isolated chlorotic spots	Highly resistant
2	Small chlorotic spots	Highly resistant
3	Chlorotic spots in rows	Resistant
4	Chlorotic splotches	Moderately resistant
5	Mild Chlorotic streaks	Moderately resistant
6	Prominent Chlorotic streaks (at least one leaf partially folded)	Moderately susceptible
7	Severe streaks, leaves partially rolled (Leaf U shaped in cross section); Emerging leaf trapped and folded	Susceptible
8	Severe streaks; severe leaf rolling	Highly susceptible
9	Plant dying	Highly susceptible

(Malinga, 2007)

CHAPTER FOUR

RESULTS AND DISCUSSION

4.1 *Diuraphis noxia* populations' host preference and performance on selected wheat genotypes

4.1.1 Host preference

Aphid preference varied significantly with host genotype (Figure 5). Compared to other genotypes, Kwale was most preferred by all the aphid populations. For example, 24 hours after infestation, an average of 42 aphids had settled on Kwale compared to 12, 10 and 8 on AUS9, AUS7 and KRWA9 respectively. This indicates an antixenotic effect of the resistant varieties to the Russian wheat aphid populations. The resistant genotypes exhibiting antixenosis may have preformed plant features and toxic compounds in or on the plant prior to infestation (Kelman and Sequeira 1972), or inert chemicals that are rapidly made toxic following infestation (Karban and Myers 1989). This was however not explored in this study and remains to be determined if indeed the resistance in these genotypes were based on preformed defenses to deter RWA colonization.

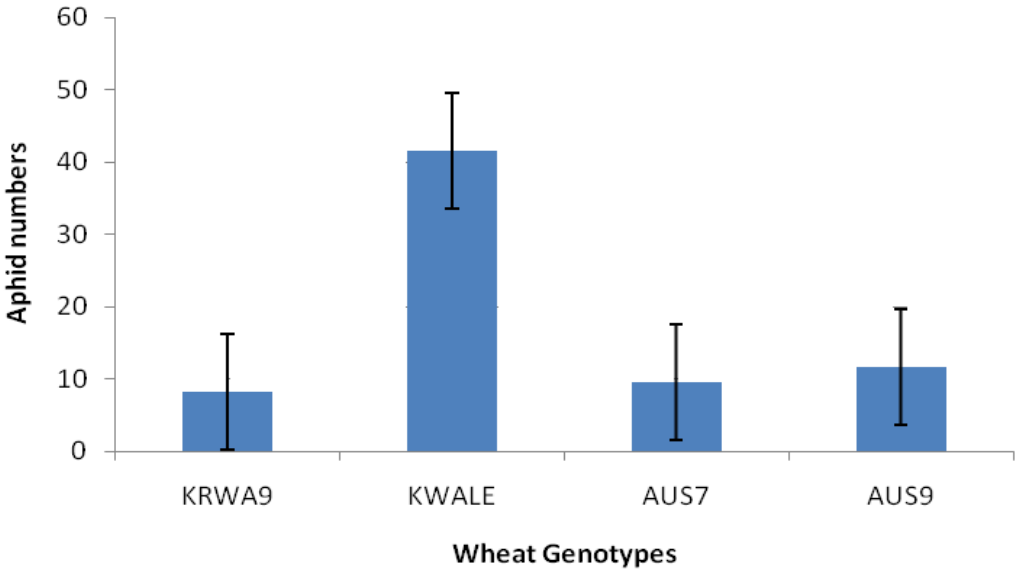


Figure 5. Host preference by *Diuraphis noxia* populations

There were significant differences in the aphid populations' host selection. The most successful RWA population in host selection and colonization was Eldoret population followed by Njoro population and last were Egerton and Mau Narok population (Table 4). This indicates that Eldoret population would colonize wheat despite the presence of a resistance gene in the wheat. This population is non selective and would thrive in both resistant and susceptible wheat and therefore requires more aggressive management through integrated management where a variety of management strategies are used together with HPR in order to manage this population.

There was significant population-genotype interaction in the population choice of host (Table 5). Kwale a susceptible genotype had no antixenosis hence was located by most RWA populations. KRWA9 had higher antixenosis for Egerton population as compared to Njoro, Mau Narok and Eldoret populations. All resistant host genotypes expressed antixenosis against all RWA populations tested except AUS9 which did not show antixenosis against Mau Narok population.

Table 4. Russian wheat aphid, *Diuraphis noxia* populations host colonization preference

RWA Population	% Released aphids counted on host
EGERTON	13.5
ELDORET	22.4
MAU NAROK	16.7
NJORO	18.5
LSD	3.8
CV	31.6

Table 5. Interaction of wheat genotype and RWA population on RWA preference for wheat host 24 hours after infestation.

	APHID POPULATION			
GENOTYPE	EGERTON	ELDORET	NJORO	MAU NAROK
KWALE	29.3	53.3	50.0	33.7
KRWA9	3.3	12.3	10.0	7.3
AUS7	12.7	13.3	7.7	5.0
AUS9	8.7	11.0	6.33	20.7
LSD	6.48	33.1	6.7	14.2
CV	24.0	10.2	18.2	42.6

Insect herbivores use several strategies to exploit hosts. Host selection is a fitness trait that increases herbivore efficiency and performance (Karban and Agrawal, 2002). Several host plant characteristics mediate the choice of wheat genotype as a suitable host to aphids. All resistant genotypes showed antixenosis to specific RWA populations and therefore could be used in the management of the aphid in Kenya, AUS9 which did not show strong antixenosis towards Mau Narok RWA population would not be a good candidate for management of RWA through host plant resistance in Mau Narok region since it would not deter RWA colonization. The specific features that make the resistant hosts to be antixenotic to RWA could not be determined in this study, however, plant volatiles emitted by the host plant that act as either insect repellants or feeding deterrents (Klueken *et al.*, 2008; Ninkovic and Ahman, 2009) or plant surface characteristics such as glandular trichomes which increases colonizing aphids mortality through entrapment and hampered movement (Fernandez, 1994; Walling, 2008) could be among plant characteristics that make the resistant genotypes to be antixenotic to RWA. There is need for further studies to determine the usefulness of antixenotic effect of these genotypes in the management of RWA.

Natural selection will favor herbivores that are selective about the food they ingest. Ecologically, successful invaders or colonizers such as RWA choose the most suitable host or actively induce changes in plant metabolism for their own benefit, these cause metabolic changes that subvert plant resistance responses directed at impairing aphid metabolism (Giordanengo *et al.*, 2010). It can be inferred that the Mau Narok RWA population is a very efficient in colonizing AUS9 thus effective management would depend on careful choice *Dn* resistance genes to deploy in that wheat region.

4.1.2 Population growth of RWA populations on different wheat genotypes

The three populations differed significantly in survivorship on the two wheat genotypes. Eldoret and Mau Narok populations had a characteristic Type II survivorship curve with constant mortality across all ages (Figure 6 and 7). Njoro population however had high mortality towards its maximum lifetime giving a characteristic Type I survivorship curves (Figure 8). Maling'a *et al.* (2007) noted a similar mortality trend for Njoro population. Njoro population had low mortality among its young compared to the Eldoret and Mau Narok populations. The difference is probably because the prevailing temperature in the greenhouse (mean temperature 25.8^0C,) may have been more favourable for Njoro population which is adapted. Njoro has lower altitude (2166 masl) compared to both Mau Narok (2829 masl) and Eldoret (2180 masl). Michels and Behle (1988) found that mortality of RWA increased with increase in temperature.

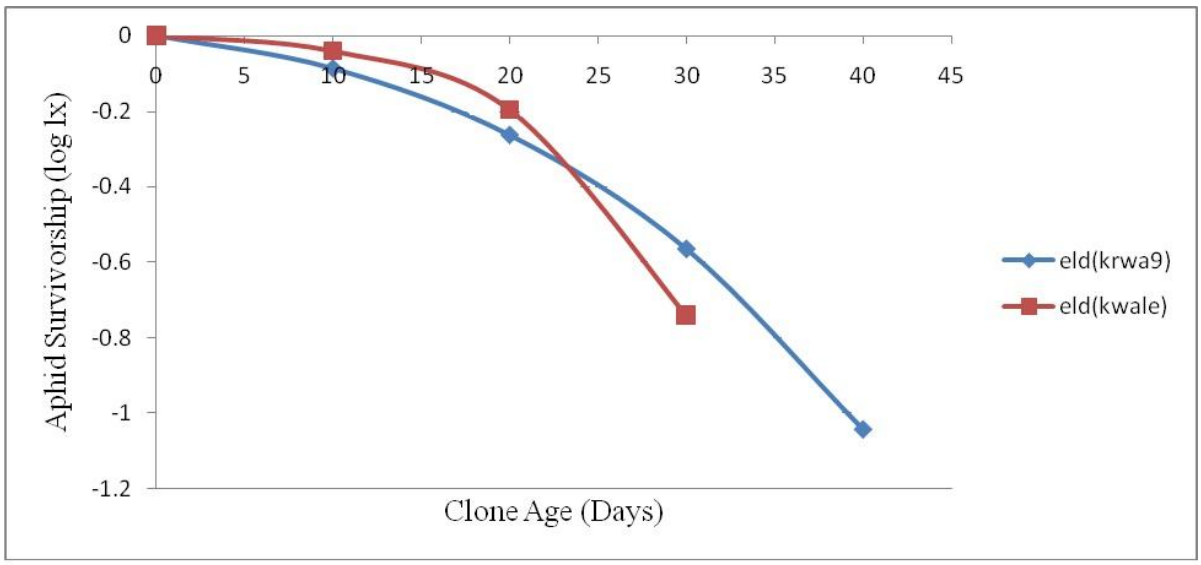


Figure 6. Survivorship curves for Eldoret RWA population on Kwale and KRWA9

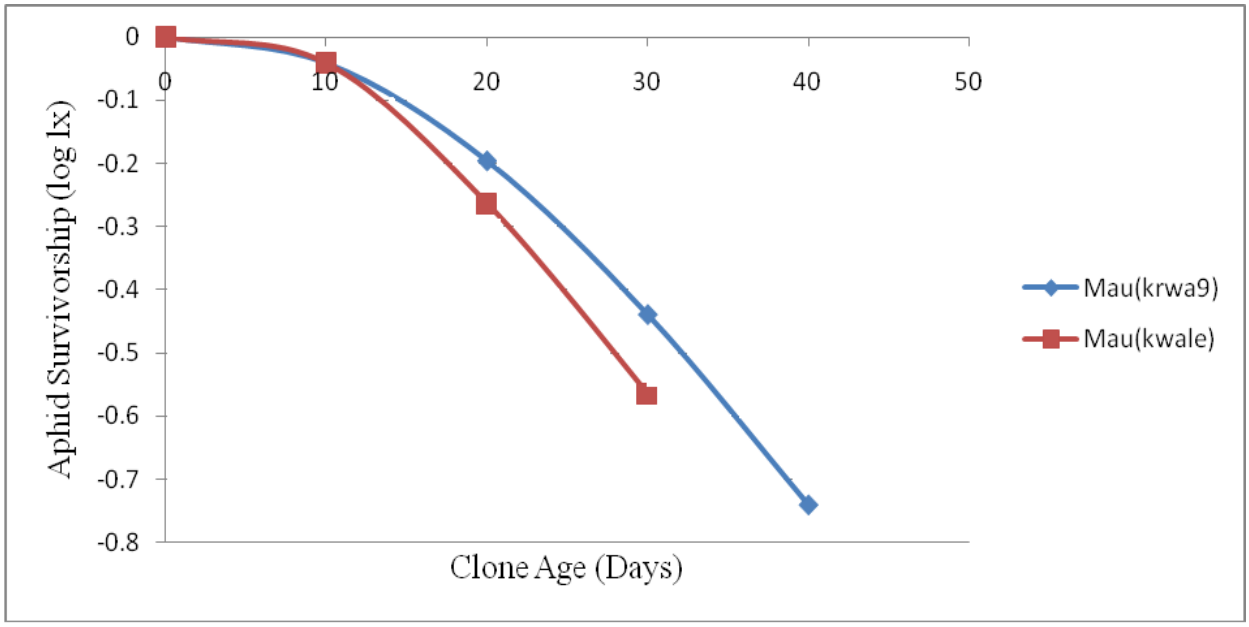


Figure 7. Survivorship curves for Mau Narok RWA population on Kwale and KRWA9

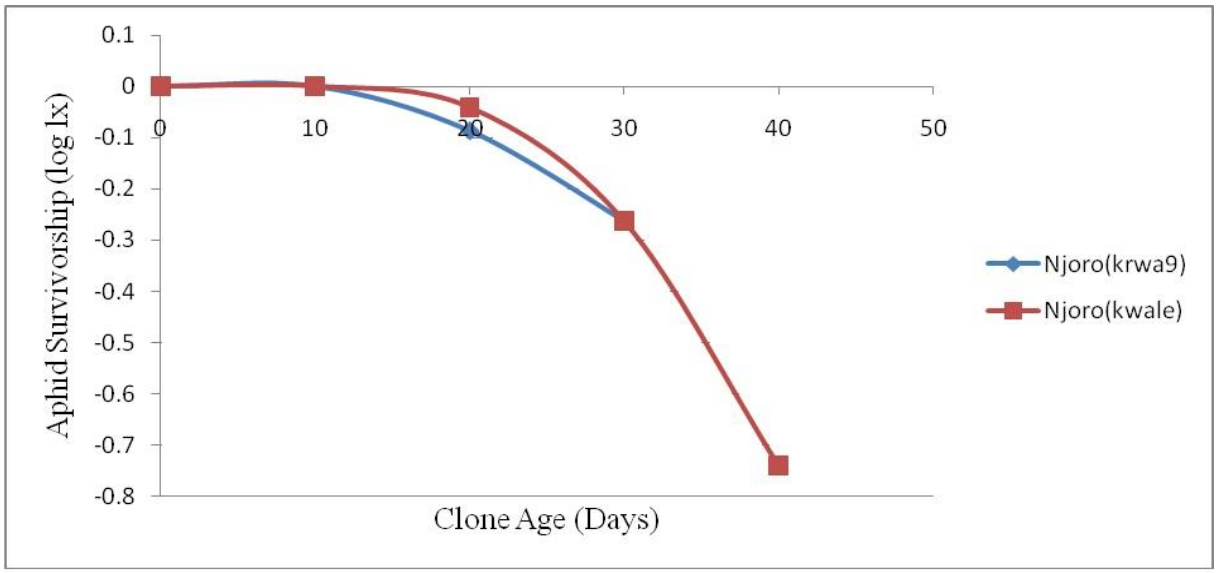


Figure 8. Survivorship curves for Njoro RWA populations on Kwale and KRWA9

The aphid populations did not differ in their development time (the time from birth to first reproduction). The wheat genotypes however had a significant effect on the development time of populations of RWA. The aphids took only 9.7 days to reach reproduction on wheat genotype Kwale compared to 10.8 days on resistant wheat line KRWA9 (Table 6).

Primary and secondary metabolites found in plant phloem exudates influences aphid development and reproduction (Awmack and Leather, 2002; Khan and Port, 2008). Resistant plants contain higher levels of antibiotic secondary metabolites such as hydroxamic acids that reduce insect attack (Niemeyer, 1988). Agrawal, (2004) found that nitrogen content was a limiting factor in aphid population growth, because the higher percentage of carbon in the phloem makes it more difficult for aphids to extract nitrogen and therefore limits population growth. Kwale did not have RWA resistance and was more suitable for aphid development compared to KRWA9. Aphid populations took a significantly shorter time to develop on Kwale compared to KRWA9.

Table 6. Effect of host genotype and aphid population on development time of RWA

VARIETY	DEVELOPMENT TIME (DAYS)				
	1st Instar	2nd Instar	3rd Instar	4th Instar	Dev. Time
KRWA9	4.30	2.50	2.10	2.00	10.80
KWALE	3.70	2.10	2.10	2.30	9.70
SE	0.12	0.11	0.08	0.08	0.35
CV	4.60	10.00	4.60	9.20	5.60

There was significant host-population interaction on development time of first and second instar of RWA (Table 7). Development time of first instar of Mau Narok and Njoro population was significantly different from the Eldoret population. Development time of the second instar of Mau Narok RWA population was significantly longer compared to Eldoret and Njoro RWA populations which had similar development time on Kwale. Overall development differed significantly among RWA populations on Kwale. Eldoret RWA population had the shortest development time on Kwale compared to Mau Narok and Njoro populations whose development time was similar on Kwale. There were no differences in development time of RWA populations on KRWA9 (Table 7).

First, second and third instars of Mau Narok population were observed to be indifferent to the effect of variety on development time (Figure 9). However, significant differences were observed during the fourth instar with KRWA9 taking a shorter time to attain maturity. This result indicates that Mau Narok population was affected by nutrients present in KRWA9 causing it to try to develop a survival mechanism.

There was no host by population interaction on the development time of the third and fourth instars of all tested RWA populations (Table 7). The results observed are consistent with findings by Aalbersberg *et al.* (1987); Kazemi *et al.* (2001); Maling'a *et al.* (2007) and Merrill *et al.* (2009). .

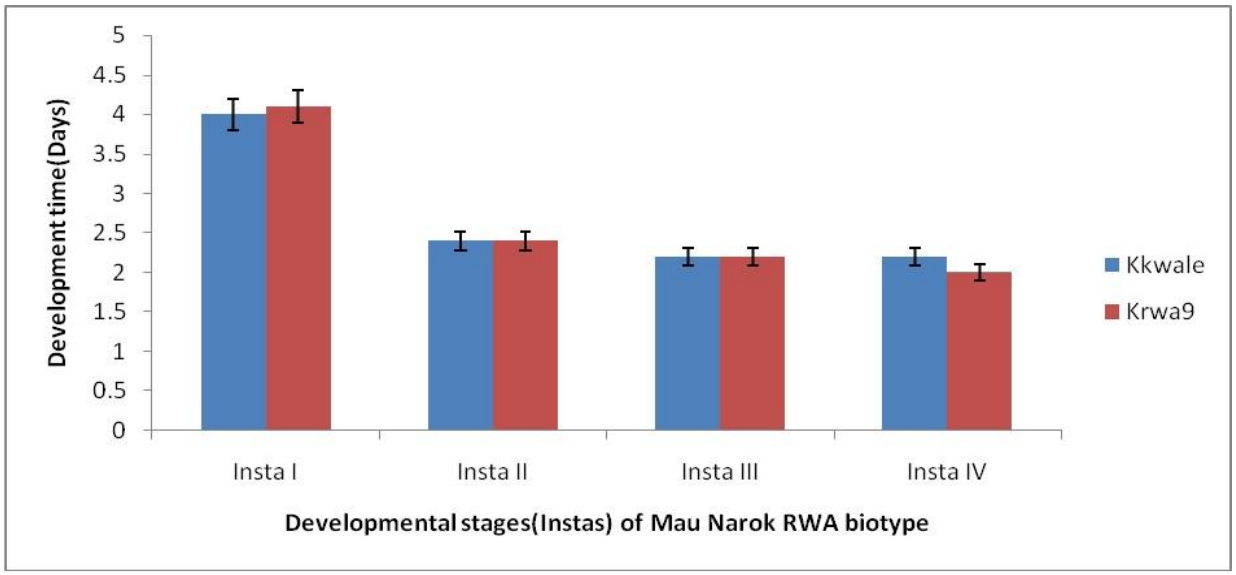


Figure 9. Development time of instars of Mau Narok RWA population on Kwale and KRWA9

Table 7. Effect of two wheat genotypes on development (days) of RWA populations

POPULATION	DEVELOPMENT TIME (DAYS)									
	1^{ST} Instar		2^{ND} Instar		3^{RD} Instar		4^{TH} Instar		Dev. Time	
	KWALE	KRWA9	KWALE	KRWA9	KWALE	KRWA9	KWALE	KRWA9	KWALE	KRWA9
ELDORET	3.50	4.30	1.80	2.50	2.00	1.90	2.20	2.00	8.80	10.60
MAU NAROK	4.00	4.10	2.40	2.40	2.20	2.20	2.20	2.00	10.40	10.30
NJORO	3.60	4.50	2.00	2.50	2.00	2.20	2.40	2.10	10.00	11.50
SE	0.20	0.22	0.16	0.17	0.10	0.17	0.15	0.07	0.43	0.64
CV	12.5	12.2	18.7	15.8	11.4	19.3	16.3	9.00	14.0	14.0

Wheat genotypes did not significantly affect the reproduction time and lifespan of aphids. Host genotype however significantly affected the Md (fecundity in a time equivalent to development time), and total aphid fecundity. Genotype Kwale was the most suitable host as shown by the high number of progeny produced on it (Table 8). Qing-Nian *et al.* (2009) similarly noted that resistant wheat genotypes significantly decreased the population growth of the grain aphid *Sitobian avenae.* Oviposition behavior of herbivorous insects responds to host quality and availability (Papaj, 2000). All populations had significantly higher total fecundity and Md (Fecundity at a time equivalent to the development time) on Kwale, a susceptible host compared to resistant genotype KRWA9. This indicates that KRWA9 has antibiosis as the mode of resistance since it affects aphid biology. The high increase in population during a time equivalent to development time has been cited as critical to determining individual contribution to the population of an aphid species because aphids contribute almost 90% of the progeny to population during this period (Wyatt and White, 1977; Migui, 1996).

Table 8. The effect of wheat genotype on the reproduction time, total aphid lifespan, mean daily fecundity, md and total fecundity of RWA.

HOST GENOTYPE	REPRODUCTION TIME (DAYS)	APHID LIFESPAN (DAYS)	M_d	TOTAL FECUNDITY (NYMPHS/FEMALE)
KRWA9	16.9	26.2	15.6	23.4
KWALE	18.3	26.7	19.8	31.2
SE	2.1	2.4	1.7	3.4
CV	28.1	20.3	18.3	25.9

There were significant differences in aphid reproductive time, total aphid lifespan, md (fecundity in a time equivalent to the aphid development time) and total aphid fecundity between aphid populations (Table 9). Njoro population produced a significantly higher number of progeny and had the longest reproduction time compared to Mau Narok and Eldoret populations.

Table 9. The differences in reproduction time, total aphid lifespan, mean daily fecundity, fecundity at md and total fecundity of RWA populations

RWA POPULATION	Reproduction Time (Days)	Aphid Lifespan (Days)	M_d	Total Fecundity (Nymphs/Female)
ELDORET	15.2	22.9	17.6	26.8
MAU NAROK	14.6	23.6	15.2	21.2
NJORO	23.1	32.8	20.4	33.6
SE	2.6	3.0	2.0	4.2
CV	28.1	20.3	18.3	25.9

Njoro population had a higher reproductive longevity and fecundity than Eldoret and Mau Narok populations (Table 9). Njoro and Eldoret populations had higher number of progeny at a duration equivalent to its development time (Md), compared to Mau Narok The differences in total aphid fecundity can be attributed to differences in aphid populations, wheat genotypes and the longevity of reproductive time.

There was no host by population interaction on reproduction time, total lifespan, daily fecundity and Fecundity of a time equivalent to the development time of RWA. However, there was host by population interaction on total fecundity. Eldoret and Njoro populations had the highest fecundity on Kwale while Njoro and Mau Narok populations had the highest progeny on KRWA9. Eldoret population however had the lowest progeny on KRWA9 indicating that this genotype may be effective in managing population build up of Eldoret population of RWA (Table 10).

Diehl and Bush (1984) defined nonspecific, sympatric populations which differ in some biological traits as biotypes. Longevity of reproductive time, Aphid lifespan and total aphid fecundity of aphid populations clearly show Njoro population to be a distinct biotype of RWA in Kenya.

Table 10Effect of host genotype (Kwale and KRWA9) on the reproduction time (days), total aphid lifespan(days), daily fecundity, md and total fecundity of populations of RWA.

	Reprodution Time (RT) days		Aphid Lifespan (l)days		M_d		Total Fecundity (TF) (Nyphs/Female)	
RWA Population	KWALE	KRWA9	KWALE	KRWA9	KWALE	KRWA9	KWALE	KRWA9
ELDORET	18.4	11.5	23.8	22.0	20.1	14.3	35.6	16.7
MAU	12.5	17.4	21.7	25.5	15.1	15.8	18.2	24.7
NAROK NJORO	24.5	21.1	34.5	31.0	23.7	17.1	38.9	28.0
SE	3.7	2.8	4.3	3.7	3.3	2.3	7.5	4.0
CV	47.0	39.3	38.0	32.9	39.4	34.4	56.7	40.0

Table 11. Effect of host genotype and aphid population on the Intrinsic rate of increase and the cohort generation time of Kenyan populations of the RWA.

HOST	Intrinsic Rate of Natural Increase (*Rm*)	Cohort Generation Time (*Tc*) Days
KRWA9	0.18	14.34
KWALE	0.21	12.97
SE	0.01	0.47
RWA POPULATION		
ELDORET	0.20	12.91
MAU NAROK	0.17	13.76
NJORO	0.21	14.30
SE	0.02	0.57
CV	11.60	5.60

All aphid populations had a positive intrinsic rate of population increase indicating their ability to build up populations. There was significant effect of wheat genotype and aphid population on intrinsic rate of natural increase of the populations. The aphid populations were however not different from each other when intrinsic rate of natural increase was compared and when cohort generation time was compared (Table 11). The interaction between host genotype and aphid population was not significant on the intrinsic rate of natural increase of RWA populations and cohort generation time of RWA. Genotype Kwale had the biggest effect on intrinsic rate of natural increase compared to KRWA9 and was the best host for increasing the aphid population of RWA. Maling'a (2007) reported that the aphid populations developed faster and higher populations on susceptible wheat genotypes without *Dn* genes as compared to resistant wheat genotypes like KRWA9 that contained *Dn* genes and its progenies. This shows that resistant wheat genotypes that contain *Dn* genes can be used to manage RWA populations in Kenya.

Pearson's correlation coefficients for aphid development time, aphid reproductive time (reproduction longevity), aphid lifespan, Md, Total fecundity, Intrinsic rate of natural increase and Cohort generation time are presented in Table 12. Significant negative relationship was observed between aphid development time and Md ($r=0.299$, $p<0.05$) indicating that populations with shorter development time had higher progenies during the initial reproduction period. Development time was also negatively correlated with total fecundity and intrinsic rate of natural increase. This means that the aphid population with the shortest development time has a higher intrinsic rate of natural increase and total fecundity. Cohort generation time was negatively correlated with md, total fecundity and intrinsic rate of natural increase meaning that these parameters cannot be used to predict cohort generation time of RWA.

Reproductive time had significant positive correlation with aphid lifespan, md, total fecundity and intrinsic rate of natural increase. Aphid lifespan was positively correlated with Md, total fecundity and intrinsic rate of natural increase. Whereas Md was strongly correlated with total fecundity and intrinsic rate of natural increase which is expected.

There was no correlation between Development time, reproductive time, aphid lifespan and cohort generation time.

Table 12 Correlation matrix for aphid development time, aphid reproductive time, aphid lifespan, Md, Total fecundity, Intrinsic rate of natural increase and Cohort generation time

	Dtime	Rtime	Lifespan	Md	Fecundity	Rm	Tc
Dtime	1.000						
Rtime	-0.099	1.000					
Lifespan	0.007	0.994*	1.000				
Md	-0.299*	0.773*	0.749*	1.000			
Fecundity	-0.321*	0.897*	0.868*	0.886*	1.000		
Rm	-0.529*	0.673*	0.624*	0.921*	0.800*	1.000	
Tc	1.000	-0.098	0.008	-0.298*	-0.321*	-0.529*	1.000

r (0.05,64)=0.250

*significant correlation at p=0.05

4.2 Virulence of Kenyan populations of *Diuraphis noxia* on seedlings of selected lines of wheat

4.2.1 Plant damage score

There were significant differences in damage level on wheat genotypes at different duration of RWA infestation. Wheat genotypes developed RWA damage symptoms as early as seven days post infestation. (Figure 10). Maling'a (2007) similarly found that symptoms of damage started to manifest in both resistant and susceptible plant entries as early as seven days after first infestation, thus for effective management, control should start early.

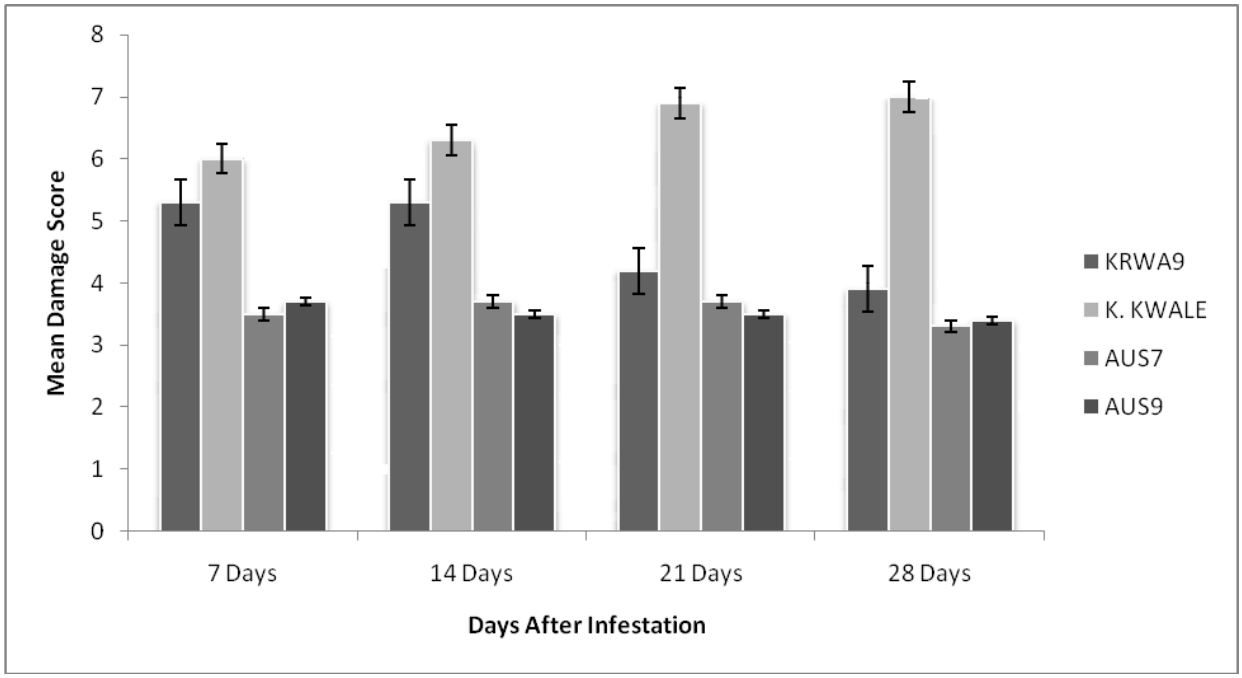


Figure 10. Mean plant damage values on wheat at various days after infestation with *Diuraphis noxia*.

Wheat genotype varied significantly in damage resulting from RWA populations on all days. Wheat genotype Kwale was generally susceptible throughout the period with susceptibility increasing over time while wheat KRWA9, AUS 7 and AUS 9 were moderately resistant (Figure 10). KRWA9 had initially moderate resistant scores of 5.2 for 14 days but scores declined after 21

days to give readings of 3.8 means. This suggests that KRWA9 has some internal factors that enables it to overcome infestation. The AUS lines 7&9 exhibited a similar trend but not as severe.

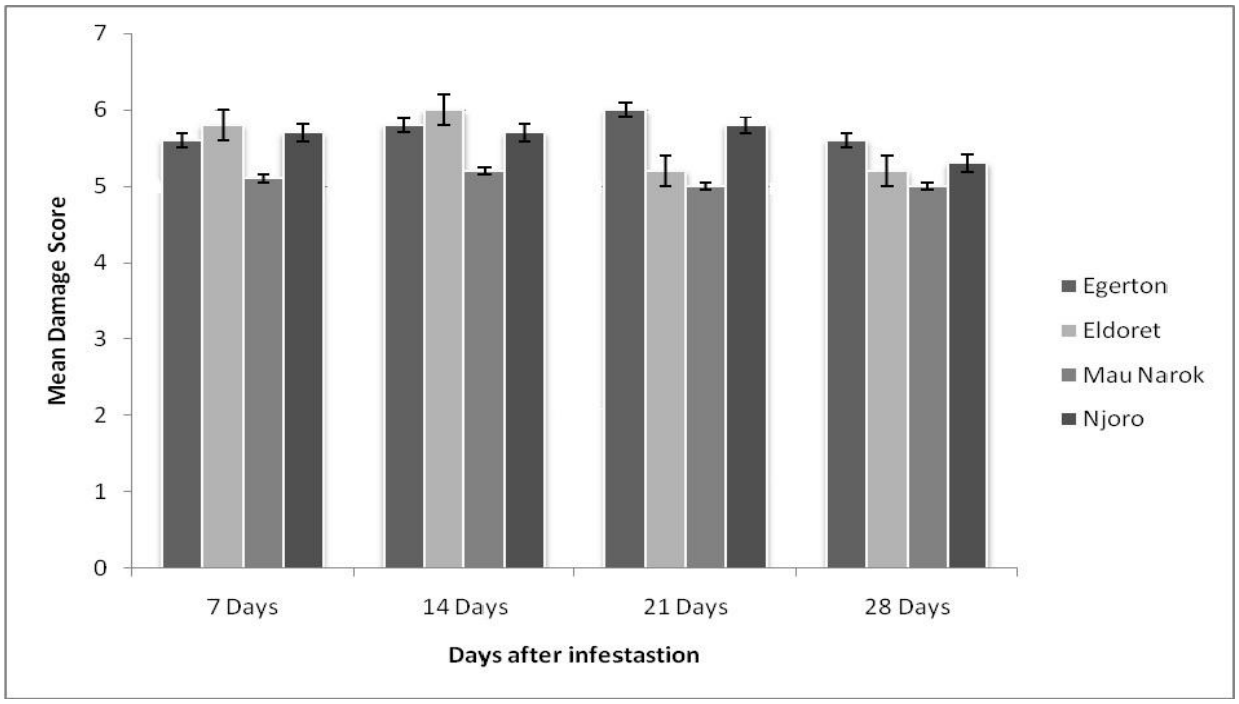


Figure 11. Mean plant damage score at varying days of wheat infestation with *Diuraphis noxia* populations.

Aphid populations caused significant damage on wheat genotypes. The populations varied significantly in their virulence on wheat genotypes (Figure 11). At 7 days post infestation, all aphid populations caused plant damage with Egerton, Eldoret and Njoro populations causing the most damage. Irrespective of wheat genotype, Mau Narok population caused the least damage on infested wheat. Twenty one days after infestation, Njoro, Egerton and Eldoret populations were the most virulent. Kiplagat (2005) similarly found that Nakuru populations' were more virulent. There was significant interaction of RWA population and Wheat genotype (Figure 12 and 13). The degree of damage varied with duration of infestation in Kwale and KRWA9. The longer the infestation period, the more severe damage was on Kwale a susceptible genotype whereas for KRWA9, the longer the infestation period, the lesser the damage.

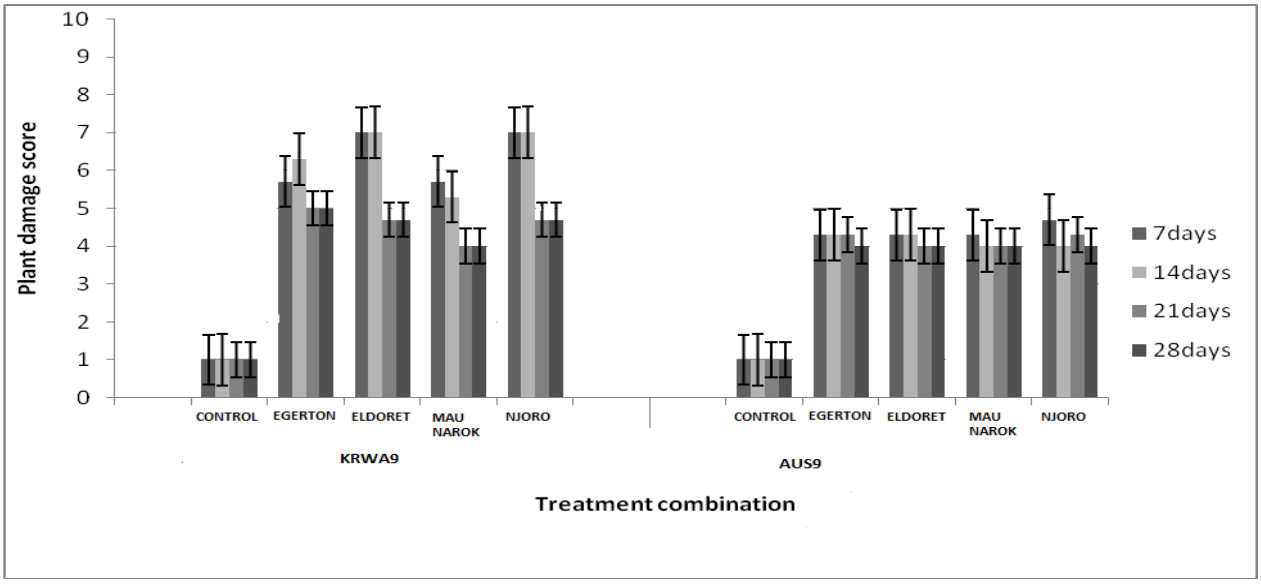


Figure 12. Level of plant damage caused by different aphid (*Diuraphis noxia)* populations on KRWA9 and AUS9 wheat genotypes at varying times of infestation

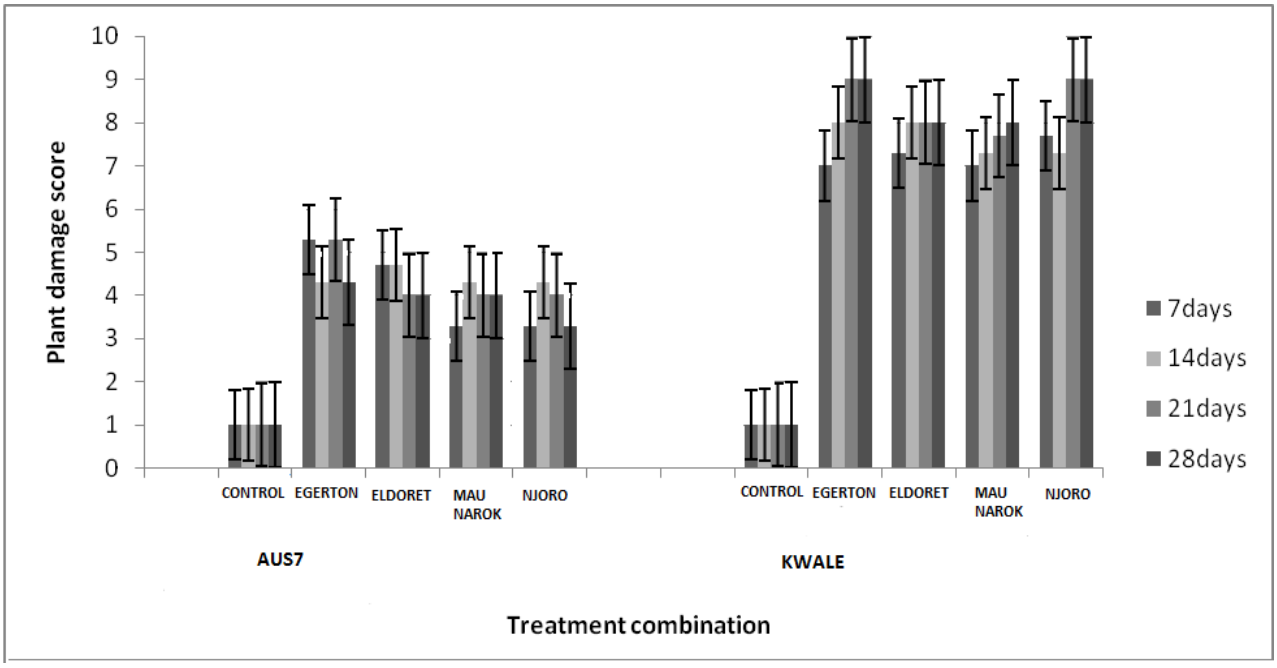


Figure 13. Level of Plant damage caused by different *Diuraphis noxia* aphid populations on AUS7 and Kwale wheat genotype at varying times of infestation

Generally, all RWA populations significantly cause damage to wheat. The degree of damage however varies with RWA population and the duration under which wheat remains infested. There were no differences among RWA populations in the amount of damage on AUS7 and AUS9 at 14, 21 and 28 days of infestation. The two wheat genotypes were moderately resistant to all RWA populations that were tested. The low damage scores could be attributed to the *Dn* resistance genes incorporated into these wheat genotypes. Significant differences in damage were noted among RWA populations on KRWA9 during the entire period of infestation. This genotype was severely damaged during the first 14 days of infestation with RWA. This trend was however reversed in the subsequent days as severity of damage symptoms lessened with increase in the duration of infestation. Njoro and Eldoret populations were the most virulent in the first 14 days of infestation. Mau Narok population was the least virulent to KRWA9 during the entire period of evaluation. KRWA9 has significantly lower mean damage score 21 and 28 days after infestation. This indicates that the *Dn* resistance gene in KRWA9 may be responsible for systemic acquired resistance observed in the genotype.

4.4.2 Effect of *Diuraphis noxia* populations on growth of selected bread wheat seedlings

Plant damage due to *Diuraphis noxia* is associated with developmental, morphological, physiological and biochemical processes in the host plant that has an impact on growth and development of wheat seedlings (Franzen *et al*., 2007). There was significant variation in seedling growth of wheat genotypes infested with *Diuraphis noxia* populations. Percent reduction in plant height varied significantly across wheat genotypes. AUS7 and AUS9 were the least stunted plants followed by Kwale and KRWA9 28 days after infestation with RWA populations (Table 13). Reduction in plant height is an important symptom of damage that is used to characterize population virulence.

Table 13. Effect of RWA (*Diuraphis noxia)* populations on growth of selected bread wheat genotype seedlings, 28 days after infestation.

Host Genotype	% Leaf number reduction	% Plant height reduction	%Fresh shoot weight reduction	%Dry shoot weight reduction
KRWA9	25.3	36.3	40.8	11.7
KWALE	27.1	25.3	25.9	7.4
AUS 7	11.0	6.8	17.4	4.4
AUS 9	20.0	7.2	15.7	6.4
LSD	8.8	1.8	2.2	2.2
CV	52.4	12.7	12.2	41.0

There was significant reduction in wheat shoot fresh and dry weight 28 days after infestation of bread wheat with *Diuraphis noxia*. AUS7 and AUS9 had the lowest height, and shoot weight reductions, an indication that these two genotypes are tolerant to RWA infestation at seedling stage. Tolerance identified in AUS7 and AUS9 is encouraging because it may delay D noxia biotype selection. Reduction in biomass of wheat plants infested with *Diuraphis noxia* has also been reported by Ni and Quinsenberry (2006) and is attributed to impaired transport of photosynthetic assimilates for growth and also the drain by aphids that consume these assimilates therefore starving the growing plant (Saheed, 2007). Reduction in plant height and weight among individual wheat genotypes arise from differential damage by RWA feeding and also genotype characteristics in relation to infestation that causes infested plants to become stunted. RWA feeding on wheat impairs the water potential of infested plants by interfering with osmotic transport in plants and therefore also interferes with cell wall extension in plant meristems and therefore causes stunting in infested plants (Saheed, 2007; Franzen *et al*., 2007)

RWA populations varied significantly in their effect on plant height 28 days after infestation. (Table 14). Egerton population is the most virulent population and caused the highest % reduction in plant height followed by Eldoret and Njoro population respectively. Mau Narok population caused the least reduction in plant height among RWA populations. There were significant

differences in % reduction in shoot fresh weight of test plants,(Table 14) Test plants infested with Egerton population had the least shoot fresh weight and the population caused the highest % fresh shoot weight reduction among RWA populations.

Table 14. Effect of RWA (*Diuraphis noxia)* populations on growth of bread wheat seedlings after for 28 days of infestation

RWA POPULATION	% Plant height reduction	%Fresh shoot weight reduction	%Dry shoot weight reduction
UNINFESTED CONTROL	0.0	0.0	0.0
EGERTON	26.9	36.4	10.0
ELDORET	24.6	29.6	10.2
MAU NAROK	20.1	28.5	8.3
NJORO	22.9	30.1	8.9
LSD	2.0	2.5	2.5
CV	12.7	12.2	41.0

There were significant two way interactions between host genotype and aphid population in some growth measurements of wheat seedlings. Significant interaction was observed in plant height reduction on wheat genotype KRWA9 (Table 15). Significant interaction was also observed in % reduction in plant height, % reduction in shoot fresh weight, and % reduction in shoot dry weight on Kwale, AUS7, and AUS9, (Tables, 15 and 16).

Table 15. Effect of RWA (*Diuraphis noxia)* population on KRWA9 and AUS9 wheat genotype seedling height, shoot fresh weight and dry weight reduction 28 days after infestation

	KRWA9			AUS 9		
RWA Population	**% Plant height reduction**	**%Fresh shoot weight reduction**	**% Dry shoot weight reduction**	**% Plant height reduction**	**%Fresh shoot weight reduction**	**% Dry shoot weight reduction**
UNINFESTED	0.0	0.0	0.0	0.0	0.0	0.0
EGERTON	53.3	52.3	15.0	15.8	25.6	7.5
ELDORET	40.9	50.4	14.8	7.1	13.4	9.5
MAU NAROK	47.1	50.8	14.7	5.2	25.3	7.5
NJORO	40.1	50.2	14.1	7.9	14.0	7.4
LSD	4.9	3.1	4.9	4.5	4.7	4.7
CV	7.2	4.1	22.3	32.9	15.8	38.8

Table 16. Effect of RWA (*Diuraphis noxia)* population on Kwale and AUS7 wheat genotype seedling height, shoot fresh weight and dry weight reduction 28 days after infestation

	KWALE			AUS 7		
RWA Population	**% Plant height reduction**	**%Fresh shoot weight reduction**	**% Dry shoot weight reduction**	**% Plant height reduction**	**%Fresh shoot weight reduction**	**% Dry shoot weight reduction**
UNINFESTED	0.0	0.0	0.0	0.0	0.0	0.0
EGERTON	29.1	36.2	9.8	9.5	31.5	7.8
ELDORET	42.6	32.6	11.2	7.7	21.9	5.3
MAU NAROK	23.1	23.5	6.4	4.9	14.5	4.6
NJORO	31.4	36.9	9.7	12.0	19.2	4.2
LSD	4.5	4.8	4.8	3.2	2.9	3.5
CV	9.5	34.2	34.2	24.7	8.8	42.6

4.4.3 Pearsons Correlation between RWA damage and growth of wheat seedlings

Results on Pearsons' correlation coefficients among parameters of wheat infested with RWA and RWA damage scores at 7, 14, 21, and 28 days in the greenhouse are presented in Table 17. Significant positive associations were observed between damage score and plant height reduction, shoot fresh weight reduction and shoot dry weight reduction. Russian wheat aphid infestation of wheat results in stunted growth and reduced straw weight. A significant negative relationship exists between damage scores and plant height, shoot fresh weight and shoot dry weight.

Table 17. Correlation matrix for damage score, plant height, plant height reduction, shoot fresh weight, shoot fresh weight reduction, shoot dry weight and shoot dry weight reduction

	First score	Second score	Third score	Fourth score	Plant height	Plant height reduction	Shoot fresh weight	Shoot fresh weight reduction	Shoot dry weight	dry weight reduction
First score	1									
Second score	0.91*	1								
Third score	0.87*	0.92*	1							
Fourth score	0.84*	0.90*	0.98*	1						
Plant height	-0.72*	-0.75*	-0.63*	-0.612*	1					
Plant height reduction	0.76*	0.78*	0.63*	0.602*	-0.947*	1				
Shoot fresh weight	-0.77*	-0.79*	-0.71*	-0.670*	0.631*	-0.721*	1			
Shoot fresh weight reduction	0.81*	0.80*	0.65*	0.593*	-0.825*	0.904*	-0.824*	1		
Shoot dry weight	-0.75*	-0.77*	-0.71*	-0.682*	0.668*	-0.716*	0.872*	-0.749*	1	
Shoot dry weight reduction	0.71*	0.66*	0.56*	0.511*	-0.697*	0.768*	-0.608*	0.829*	-0.633*	1

$r_{(0.05,58)}=0.273$

*significant correlation at p=0.05

Table 18 provides a summary of the study and suggests that all the lines are currently moderately resistant and would need to be pyramided if they have to be effective over a long period of time.

Table 18. A summary of the reaction of wheat genotypes against the four RWA Populations

Genotypes	Eldoret Population	Mau Narok Population	Njoro Population	Egerton Population
KWALE	S	S	S	S
KRWA9	MR	MR	MR	MR
AUS7	MR	MR	R	MR
AUS9	MR	MR	MR	MR

CHAPTER FIVE

CONCLUSIONS AND RECOMMENDATIONS

5.1 Host preference for Kenyan RWA populations

The study showed that there was significant variation in host genotype preference among kenyan RWA populations. Kwale a susceptible host, was the most preferred genotype by all RWA populations. Among the resistant genotypes, AUS9 which contains *Dn*7 resistance gene was most preferred. AUS9, is an important source of RWA resistance worldwide, Its introduction and use within the crop improvement programme should be augmented with other genes for effective success in breeding. However, individual populations of RWA had differing preference for specific host genotypes. The reason for the variation in host preference among RWA population for susceptible and resistant genotypes is not clearly understood and needs to be investigated further if the use of host plant resistance for RWA management is to be successful.

5.2 Effect of RWA population and host genotype on RWA development and population growth in Kenya

The study found variation in survivorship of RWA populations in Kenya. Mau Narok and Eldoret RWA populations had constant mortality across all ages whereas Njoro RWA population had high mortality towards the end of its maximum lifespan. As a result Njoro population had a significantly longer reproduction time, lifespan and gave birth to more nymphs compared to Eldoret and Mau Narok RWA populations indicating it was most virulent having adapted to its environment. There were no significant differences in intrinsic rates of natural increase and cohort generation time but in all parameters measured. The study showed that RWA collected from Eldoret, Mau Narok and Njoro differed in growth and reproductive potential especially on susceptible host Kwale as compared to resistant KRWA9 where no differences in growth and reproductive potential was noticeable.

Strong and positive correlation was found between aphid lifespan and reproductive time, total fecundity and intrinsic rate of natural increase. These are reliable predictors of aphid population growth. Significant negative correlation was found between cohort generation time and total aphid fecundity and reproductive time

5.3 Variation in virulence of RWA populations on wheat genotypes

The study showed that RWA damage varied between host genotypes and between RWA populations under study. This suggests that location specific resistant variety development should be undertaken. All the resistant genotypes showed intermediate resistance to RWA population though the damage varied between genotypes. AUS7 and AUS 9 emerged as strong candidates to be used in a breeding program targeting RWA populations in Eldoret and Njoro. Mau narok RWA population was not as virulent as the others on resistant genotypes. Though the variation in virulence was noted for specific host genotypes, there is need to conduct a wholesome study using all differentials for determining biotypic variation in *Diuraphis noxia* populations.

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APPENDICES

Appendix 1: **The known *Dn* genes, sources and their chromosomal locations.**

Source of resistance	Wheat Type	Chromosomal location	Origin of accession	Resistance gene	Mode of resistance
PI 137739	Hard White Spring	7D (Schroeder-Teeter et al., 1994)	Iran (Du Toit, 1987)	*Dn1*	Antibiosis and antixenosis (Du Toit 1987, 1989a)
PI 262660	Hard White Winter	7DL (Ma et al., 1998)	Bulgaria (Du Toit, 1987)	*Dn2*	Antibiosis and antixenosis (Du Toit 1987, 1989a)
Triticum tauschii	-	-	SQ24 (Nkongolo et al., 1991a)	*Dn3*	
PI 372129	Hard Red Winter	1DS	Former Soviet Union (Nkongolo et al. 1991b; Saidi and Quick, 1996).	*Dn4*	Tolerance (Saidi and Quick, 1996)
PI 294994	Hard Red Winter	7DL (Du Toit, 1987; Marais and Du Toit, 1993)	Bulgaria (Marais and Du Toit, 1993)	*Dn5*	Tolerance, antibiosis and antixenosis (Du Toit 1987, 1989b Smith et al., 1992)
PI 243781	Winter wheat	7DS	Iran (Saidi and Quick, 1996)	*Dn6*	Tolerance and Antibiosis (Miller et al., 2003
Rye accession	-	Transferred to 1RS in wheat (Liu et al., 2001)	-	*Dn7*	Antixenosis (Kogan and Ortman, 1978)
PI 294994	Hard Red Winter	7D (Liu et al., 2001)	Bulgaria (Marais and Du Toit, 1993)	*Dn8*	-

PI 294994	Hard Red Winter	1D (Liu et al., 2001)	Bulgaria (Marais and Du Toit, 1993; Liu et al., 2001)	*Dn9*	-
PI 220127	Winter wheat	7D (Liu et al., 2001)	Afghanistan (Harvey and Martin, 1990)	*Dnx*	-
PI 220350	Chinese wheat Lin-Yuan207	1DL (Liu., 2001)	China(Liu, 2001)	*Dny*	-

Appendix 2: Growth stages of small grains

CODE	Description	CODE	Description
0	**GERMINATION**	37	Flag leaf just visible
00	Dry seed	38	Flag leaf ligule just visible
01	Start of imbibitions	**4**	**BOOTING**
03	Imbibition complete	41	Flag leaf sheath extending
05	Radicle emerged from seed	43	Boots just visible swollen
07	Coleoptile emerged from seed	45	Boots swollen
09	Leaf just at coleoptiles tip	47	Flag leaf sheath opening
1	**SEEDLING GROWTH**	49	First awns visible
10	1st leaf through coleoptiles	**5**	**EAR EMERGENCE**
11	1st leaf unfolded	51	1st spikelet of ear emerged
12	2 leaves unfolded	53	One-fourth of ear emerged
13	3 leaves unfolded	55	One-half of ear emerged
14	4 leaves unfolded	57	Three-fourths of ear emerged
15	5 leaves unfolded	59	Emergence of ear completed
16	6 leaves unfolded	**6**	**FLOWERING**
17	7 leaves unfolded	61	Beginning of flowering
18	8 leaves unfolded	65	Flowering half-way complete
19	9 leaves unfolded	69	Flowering complete
2	**TILLERING**	**7**	**MILK DEVELOPMENT**
20	Main shoot only	71	Seed water ripe
21	Main shoot and 1 tiller	73	Early milk
22	Main shoot and 2 tillers	75	Medium milk (An increase in the solids of the liquid of the endosperm is notable when crushing the seed between fingers)
23	Main shoot and 3 tillers	77	Late milk
24	Main shoot and 4 tillers	**8**	**DOUGH DEVELOPMENT**
25	Main shoot and 5 tillers	83	Early dough
26	Main shoot and 6 tillers	85	Soft dough (Fingernail impression not held)

27	Main shoot and 7 tillers	87	Hard dough (Fingernail impression not held; head losing chlorophyll)
28	Main shoot and 8 tillers	**9**	**RIPENING**
29	Main shoot and 9 tillers	91	Seed hard (difficult to divide by thumbnail)
3	**STEM ELONGATION**	92	Seed hard (can no longer be dented by thumbnail)
30	Pseudostem erection	93	Seed loosening in daytime
31	1st node detectable	94	Over-ripe; straw dead/ collapsing
32	2nd node detectable	95	Seed dormant
33	3rd node detectable	96	Visible seed giving 50% germination
34	4th node detectable	97	Seed not dormant
35	5th node detectable	98	Secondary dormancy induced
36	6th node detectable	99	Secondary dormancy lost

(Adopted from Zadok *et al*., 1974)

Appendix 3: Wheat genotypes used in the study, their origins and pedigree

Sno	Genotype	Origin	Pedigree
1	K. Kwale	NPBRC, KENYA	KUZ/3/SN64/CN067////NIA66/4/MAYA//BB/INIA66
2	KRWA9	CIMMYT	84TK520.001.01//VEE#5.3/TRAP#1GRBW91.98.4-1B-3DNB-5DNH-3DNB-1DNB-3DNB
3	AUS7	USA	PI624933-1
4	AUS9	USA	2414-11-2
5	Pasa	NPBRC, KENYA	BUCKY/MAYA/4/BB/HD832/ON/3/CN067/PJ62/5/KVZ/TI/TITO

Appendix 4: Analysis of variance tables

******* Two way Analysis of variance in RCB for VARIATIONS IN HOST PREFERENCE AMONG RUSSIAN WHEAT APHID POPULATIONs.*******

Variate: Aphid_number

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
rep stratum	2	6.292	3.146	0.34	
rep.*Units* stratum					
clone	3	540.917	180.306	19.52	<0.001
variety	3	9870.250	3290.083	356.27	<0.001
clone.variety	9	1577.417	175.269	18.98	<0.001
Residual	30	277.042	9.235		
Total	47	12271.917			

******* Two way Analysis of variance in RCB for RWA performance on selected genotypes of wheat *******

Variate: Frst instar

Source of variation	d.f.	S.S.	M.S	v.r.	F pr.
Block stratum	10	2.0000	0.2000	0.90	
Variety	1	6.0606	6.0606	27.32	<.001
Clone	2	0.6364	0.3182	1.43	0.248
variety.clone	2	2.2121	1.1061	4.99	0.011
Residual	50	11.0909	0.2218		
Total	65	22.0000			

Variate: Scnd instar

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Block stratum	10	3.0909	0.3091	1.70	
Variety	1	2.9697	2.9697	16.33	<.001
Clone	2	0.3636	0.1818	1.00	0.375
variety.clone	2	1.5758	0.7879	4.33	0.018
Residual	50	9.0909	0.1818		
Total	65	17.0909			

Variate: Thrd instar

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Block stratum	10	0.5567	0.0557	0.49	
Variety	1	0.0227	0.0227	0.20	0.657
Clone	2	0.6868	0.3434	3.02	0.059
variety.clone	2	0.2069	0.1035	0.91	0.410
Residual	46(4)	5.2354	0.1138		
Total	61(4)	6.5968			

Variate: Frth Instar

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Block stratum	10	2.33360	0.23336	2.41	
Variety	1	0.86310	0.86310	8.91	0.005
Clone	2	0.25105	0.12552	1.30	0.284
variety.clone	2	0.02387	0.01194	0.12	0.884
Residual	45(5)	4.36142	0.09692		
Total	60(5)	7.67213			

Variate:Total instar development time (devtime)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Block stratum	10	19.455	1.945	0.97	
Variety	1	17.515	17.515	8.73	0.005
Clone	2	12.212	6.106	3.04	0.057
variety.clone	2	10.576	5.288	2.63	0.082
Residual	50	100.364	2.007		
Total	65	160.121			

Variate: Reproduction longevity (reprlong)

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Block stratum	10	1467.05	146.70	2.05	
Variety	1	31.29	31.29	0.44	0.512
Clone	2	986.55	493.27	6.88	0.003
variety.clone	2	399.30	199.65	2.79	0.073
Residual	44(6)	3153.94	71.68		
Total	59(6)	5688.98			

Variate:Aphid lifespan (totlong)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Block stratum	10	1723.12	172.31	1.76	
Variety	1	4.91	4.91	0.05	0.824
Clone	2	1335.12	667.56	6.80	0.002
variety.clone	2	158.82	79.41	0.81	0.451
Residual	50	4906.15	98.12		
Total	65	8128.12			

Variate: Mean daily progeny (mdalypro)

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Block stratum	10	1.6050	0.1605	0.85	
Variety	1	0.1664	0.1664	0.89	0.352
Clone	2	0.4127	0.2064	1.10	0.343
variety.clone	2	0.2079	0.1039	0.55	0.579
Residual	44(6)	8.2717	0.1880		
Total	59(6)	10.3969			

Variate: md

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Block stratum	10	636.71	63.67	1.40	
Variety	1	254.93	254.93	5.60	0.022
Clone	2	299.47	149.74	3.29	0.047
variety.clone	2	192.55	96.27	2.12	0.133
Residual	44(6)	2001.49	45.49		
Total	59(6)	3339.25			

Variate: Aphid fecundity (totpro)

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Block stratum	10	2991.5	299.2	1.53	
Variety	1	929.1	929.1	4.77	0.034
Clone	2	1695.3	847.6	4.35	0.019
variety.clone	2	1975.3	987.6	5.07	0.010
Residual	44(6)	8579.0	195.0		
Total	59(6)	15333.9			

Variate: Intrinsic rate of natural increase (rm)

Source of variation	d.f.(m.v.)	s.s.	m.s.	v.r.	F pr.
Block stratum	10	0.029854	0.002985	1.14	
Variety	1	0.010963	0.010963	4.19	0.047
Clone	2	0.016328	0.008164	3.12	0.054
variety.clone	2	0.015039	0.007519	2.88	0.067
Residual	44(6)	0.115025	0.002614		
Total	59(6)	0.184440			

Variate: Cohort Generation time (Tc)

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Block stratum	10	34.616	3.462	0.97	
Variety	1	31.106	31.106	8.70	0.005
Clone	2	21.715	10.858	3.04	0.057
variety.clone	2	18.801	9.400	2.63	0.082
Residual	50	178.678	3.574		
Total	65	284.916			

******* Two way Analysis of variance in RCB for VARIATIONS IN VIRULENCE OF RUSSIAN WHEAT APHID POPULATION *******

Variate: FIRST_SCORE

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	2.1333	1.0667	1.85	
REPS.*Units* stratum					
VARIETY	3	64.3333	21.4444	37.27	<0.001
CLONE	4	201.7667	50.4417	87.66	<0.001
VARIETY.CLONE	12	27.8333	2.3194	4.03	<0.001
Residual	38	21.8667	0.5754		
Total	59	317.9333			

Variate: SECOND_SCORE

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	0.6333	0.3167 1.50		
REPS.*Units* stratum					
VARIETY	3	80.4000	26.8000	126.77	<0.001
CLONE	4	212.5667	53.1417	251.38	<0.001
VARIETY.CLONE	12	24.1000	2.0083	9.50	<0.001
Residual	38	8.0333	0.2114		
Total	59	325.7333			

Variate: THRD_SCORE

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	0.7000	0.3500	1.11	
REPS.*Units* stratum					
VARIETY	3	113.4667	37.8222	120.10	<0.001
CLONE	4	203.0667	50.7667	161.21	<0.001
VARIETY.CLONE	12	33.2000	2.7667	8.79	<0.001
Residual	38	11.9667	0.3149		
Total	59	362.4000			

Variate: FOURTH_SCORE

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	0.3000	0.1500	0.68	
REPS.*Units* stratum					
VARIETY	3	137.7333	45.9111	208.52	<0.001
CLONE	4	175.5667	43.8917	199.35	<0.001
VARIETY.CLONE	12	38.4333	3.2028	14.55	<0.001
Residual	38	8.3667	0.2202		
Total	59	360.4000			

Variate: NUMBER_OF_LEAVES

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	0.3000	0.1500	0.63	
REPS.*Units* stratum					
VARIETY	3	0.5833	0.1944	0.82	0.492
CLONE	4	17.7333	4.4333	18.65	<0.001
VARIETY.CLONE	12	4.0000	0.3333	1.40	0.207
Residual	38	9.0333	0.2377		
Total	59	31.6500			

Variate: LEAF_RDXN

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	1362.3	681.2	5.71	
REPS.*Units* stratum					
VARIETY	3	2355.7	785.2	6.58	0.001
CLONE	4	6828.9	1707.2	14.30	<0.001
VARIETY.CLONE	12	1453.3	121.1	1.01	0.455
Residual	38	4535.8	119.4		
Total	59	16536.1			

Variate: T_LEAF_RDXN

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	0.32471	0.16236	5.81	
REPS.*Units* stratum					
VARIETY	3	0.82805	0.27602	9.88	<0.001
CLONE	4	2.52630	0.63157	22.60	<0.001
VARIETY.CLONE	12	0.34882	0.02907	1.04	0.434
Residual	38	1.06183	0.02794		
Total	59	5.08971			

Variate: PLANT_HGHT

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	4.433	2.217	0.26	
REPS.*Units* stratum					
VARIETY	3	3876.317	1292.106	152.37	<0.001
CLONE	4	1284.333	321.083	37.86	<0.001
VARIETY.CLONE	12	703.267	58.606	6.91	<0.001
Residual	38	322.233	8.480		
Total	59	6190.583			

Variate: PLANT_HGHT_RDXN

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	10.333	5.167	0.90	
REPS.*Units* stratum					
VARIETY	3	9371.602	3123.867	541.42	<0.001
CLONE	4	5653.838	1413.459	244.98	<0.001
VARIETY.CLONE	12	3257.055	271.421	47.04	<0.001
Residual	38	219.252	5.770		
Total	59	18512.079			

Variate: T_PLANT_HGHT_RDXN

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	0.004733	0.002366	1.68	
REPS.*Units* stratum					
VARIETY	3	1.706094	0.56869	402.88	<0.001
CLONE	4	2.209837	0.552459	391.38	<0.001
VARIETY.CLONE	12	0.561743	0.046812	33.16	<0.001
Residual	38	0.053640	0.001412		
Total	59	4.536047			

Variate: FRESH_WGHT

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	0.33228	0.16614	2.70	
REPS.*Units* stratum					
VARIETY	3	1.79671	0.59890	9.75	<0.001
CLONE	4	14.84464	3.71116	60.39	<0.001
VARIETY.CLONE	12	4.88061	0.40672	6.62	<0.001
Residual	38	2.33515	0.06145		
Total	59	4.18939			

Variate: FRESH_WGHT_RDXN

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	1.773	0.886	0.10	
REPS.*Units* stratum					
VARIETY	3	5904.129	1968.043	212.53	<0.001
CLONE	4	9774.640	2443.660	263.89	<0.001
VARIETY.CLONE	12	2246.789	187.232	20.22	<0.001
Residual	38	351.880	9.260		
Total	59	18279.212			

Variate: T_FRESH_WGHT_RDXN

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	0.000258	0.000129	0.10	
REPS.*Units* stratum					
VARIETY	3	0.623384	0.207795	157.60	<0.001
CLONE	4	3.411274	0.852819	646.82	<0.001
VARIETY.CLONE	12	0.299889	0.024991	18.95	<0.001
Residual	38	0.050102	0.001318		
Total	59	4.384908			

Variate: DRY_WGHT

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	0.044670	0.022335	5.83	
REPS.*Units* stratum					
VARIETY	3	0.093628	0.031209	8.14	<0.001
CLONE	4	0.356207	0.089052	23.23	<0.001
VARIETY.CLONE	12	0.064446	0.005370	1.40	0.208
Residual	38	0.145673	0.003833		
Total	59	0.704624			

Variate: DRY_WGHT_RDXN

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	157.729	78.864	8.39	
REPS.*Units* stratum					
VARIETY	3	432.397	144.132	15.34	<0.001
CLONE	4	868.462	217.116	23.11	<0.001
VARIETY.CLONE	12	148.001	12.333	1.31	0.252
Residual	38	357.081	9.397		
Total	59	1963.671			

Variate: T_DRY_WGHT_RDXN

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
REPS stratum	2	0.077860	0.038930	8.48	
REPS.*Units* stratum					
VARIETY	3	0.202626	0.067542	14.72	<0.001
CLONE	4	0.735135	0.183784	40.05	<0.001
VARIETY.CLONE	12	0.077405	0.006450	1.41	0.206
Residual	38	0.174385	0.004589		
Total	59	1.267410			