

Chapter 2

Literature Review

2.1 Introduction

The Russian wheat aphid (RWA), *Diuraphis noxia* (Mordvilko), is a serious insect pest of wheat (*Triticum aestivum*) and barley (*Hordeum vulgare*). The first published report of the aphid, as a pest on barley was by Kovalev *et al.* (1991). The aphid originated in southern Russia, countries bordering the Mediterranean Sea, Afghanistan and Iran (Walters *et al.*, 1980), but is considered a minor pest in these areas (Walters, 1984). It was first discovered in South Africa during 1978 on wheat in the northern Free State (Walters *et al.*, 1980), with severe outbreaks occurring during 1979 and 1980 (Du Toit & Walters, 1984).

Wheat is one of South Africa's major staple crops and constitutes 21% of the national arable land use together with other small grains (Marasas, 1999). The total wheat production in South Africa for the 1999/2000 season was 1.56 million tonnes (National Crops Estimates Committee, 2000). RWA infestation can result in plant yield losses of up to 90% under experimental field conditions. In yield loss trials, losses ranged from 20.6% to 91.2%, at an average of 56.8% (Hewitt, 1988). Unless preventative measures such as planting of resistant cultivars and chemical control are taken, the wheat yield loss will result in severe economic losses. The RWA caused over \$1 billion in losses to the production of small grains in the western United States since its detection in 1986 to 2000 (Porter & Webster, 2000).

Other crops damaged to a lesser extent by the RWA include oats (*Avena sativa*), rye (*Secale cereale*) and triticale (*x Triticoseale*). Many native and introduced grasses also serve as alternative

summer hosts to the RWA (Kindler & Springer, 1989). These allow the RWA to survive between wheat seasons.

2.2 Russian wheat aphid description and biology

The RWA is a small, light green aphid that is less than 2 mm in length. It can be distinguished from other aphids infesting wheat in South Africa by the short antennae and a projection above the caudal segment which gives it a “forked tail” appearance (Walters *et al.*, 1980) (Figure 2.1A).

RWA infested wheat typically has white, yellow and reddish-purple, to purple longitudinal streaks on the wheat leaves (Walters *et al.*, 1980). RWA feeding causes the double membrane of the chloroplast to be degraded after 10 days of feeding. This degradation of the chloroplast causes the characteristic streaking found on infested wheat (Fouché *et al.*, 1984). The aphids occur mainly on the new growth of the plant, in the axils of the leaves or within curled up leaves (Walters *et al.*, 1980). RWA feeding on wheat reduces growth and development of the plant, as well as a reduction in photosynthetic leaf area, which is also partly due to a combination of leaf stunting and new leaves not unfolding (Burd & Burton, 1992).

The rolling of leaves provides an optimum environment for RWA reproduction. This environment protects the RWA from contact insecticides and natural enemies that could be used as biological control agents (Miller *et al.*, 1994). Reed *et al.* (1992) showed that RWA parasitism by biological control agents was higher on plants that did not have leaf rolling. The RWA is

protected from the biological control agent by concealing itself in the enclosed leaf. Rolling of leaves during the heading stage can prevent the spike from extruding, which results in an obstruction of flowering and a consequent reduction in seed production (Miller *et al.*, 1994).

The RWA in South Africa reproduces parthenogenetically (i.e. reproduction takes place without fertilization) (Figure 2.1B). In South Africa, only winged (alate) or wingless (apterous) viviparous females are found (Walters *et al.*, 1980). Winged females are only produced when the food source is depleted or under adverse environmental conditions (Robinson, 1992). In their native countries the RWA also undergoes sexual reproduction. Males and oviparae (sexually mature females) mate to produce eggs. These eggs then overwinter during the harsh winters experienced in these countries (Kiriak *et al.*, 1990).

No sexual forms have been reported from South Africa. However, in northwestern United States, where the RWA was also introduced, occasional oviparae have been reported (Kiriak *et al.*, 1990). The term gynocyclic was proposed to explain this phenomenon whereby only the occasional oviparae but no males are produced.

The immature RWA nymph reaches maturity in approximately 10 days (Aalbersberg *et al.*, 1987; Michels & Behle, 1988; Basky & Jordaan, 1997). This is dependent on several factors of which the most important is temperature. There is a significant decrease in nymphal developmental time with increases in temperature (Aalbersberg *et al.*, 1987; Girma *et al.*, 1990). Other factors influencing nymphal developmental time are the plant growth stage and plant quality. Aphids developed much faster when feeding on the jointing stage than on any other growth stage of wheat (Girma *et al.*, 1990). The influence of plant quality has also been observed in rape plants

(*Brassica napus*), where water stressed plants increased the rate of development of the cabbage aphid, *Brevicoryne brassicae* (Miles *et al.*, 1982). RWA life span is affected by the interaction of temperature and plant growth stage. There is an increased rate of mortality as temperature and plant age is increased (Michels & Behle, 1988; Girma *et al.*, 1990).

RWA reproduction (natality) is similarly affected by temperature and plant growth stage (Michels & Behle, 1988; Girma *et al.*, 1990). Natality increased with increasing temperatures (up to 20°C) and then decreased at higher temperatures. The highest number of progeny produced was observed when aphids fed on the jointing stage of wheat. The majority of RWAs develop through five nymphal stadia (5S) before the onset of reproduction. However, some nymphs start reproducing after four (4S) or six (6S) nymphal stadia (Girma *et al.*, 1990).

Aphid density also affects RWA development. RWA placed on wheat at densities of 10 and 40 aphids per plant revealed that the plants that were initially infested with 10 aphids showed larger populations after 15 days due to higher reproduction, lower mortality and less plant death (Quisenberry & Schotzko, 1994).

It has been reported that the RWA transmits several viruses to small grain crops. These include the barley yellow dwarf virus (BYDV), barley stripe mosaic virus (BSMV), brome mosaic virus (BMV) and *Rhopalosiphum padi* virus (RhPV) (Rybicki & Von Wechmer, 1984; Von Wechmer, 1984). Damsteegt *et al.* (1992) was, however, unable to duplicate these results and found that BSMV was not transmitted by the RWA, BMV was erratically transmitted (2.5%) and BYDV was occasionally transmitted (2.8%) to plants infested with RhPV.

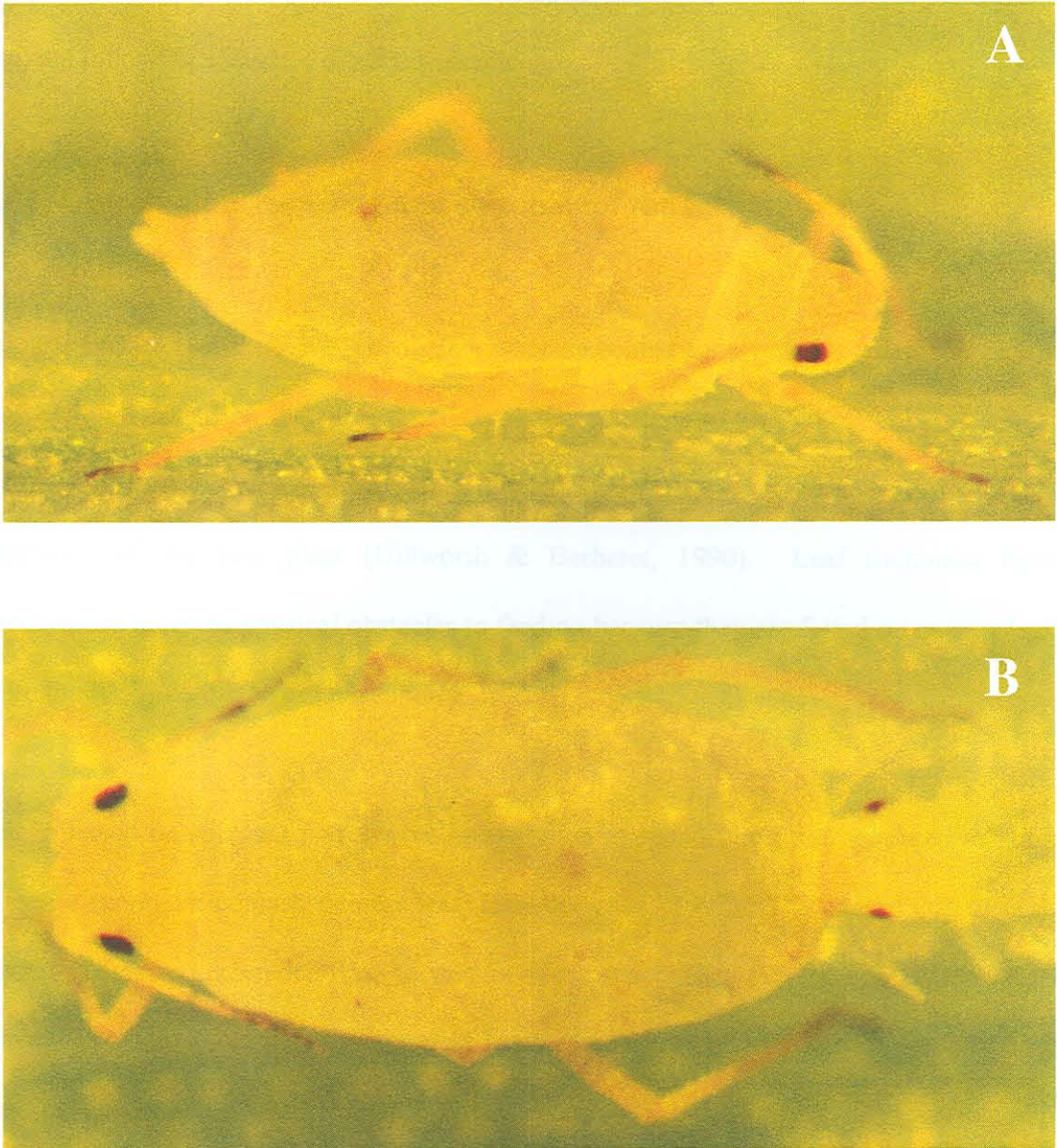


Figure 2.1. (A) The Russian wheat aphid. (B) A viviparous female Russian wheat aphid.

2.3 Feeding

The preferred host of the RWA in South Africa is wheat. Once the aphid has found a suitable host, the following sequence of action occurs:

2.3.1 Examination, probing and selection of the feeding site

The first surface that the RWA encounters when searching for a potential food source is the thin layer of lipids found on the surface known as the epicuticular wax. This covers the entire leaf surface. This wax covering is distinctive for each plant species and could play a role in RWA acceptance of the host plant (Dillworth & Berberet, 1990). Leaf trichomes have been hypothesized to act as physical obstacles to feeding because they are found on or near leaf veins, where the RWA feeds (Ni & Quisenberry, 1997b).

Aphids placed on resistant plants have been shown to spend more time engaged in nonfeeding behaviour (no stylet contact with the leaf) (Kindler *et al.*, 1992). This means that the aphids on resistant plants require more time to initiate feeding activities (Webster *et al.*, 1993). These indicate a physiological or morphological basis for the resistance observed. A RWA resistant wheat line, plant introduction (PI) 137739 was found to have the longest trichomes in comparison to two RWA susceptible wheat cultivars, 'Arapahoe' and 'Halt'. 'Arapahoe' and 'Halt' had the shortest trichomes but the highest trichome density. Trichomes are found on or near leaf veins and therefore long trichomes are likely to be an important physical obstacle as the phloem-feeding RWA probes close to leaf veins. The epicuticular wax ultrastructure was not found to

play a significant role on aphid-host preference (Ni & Quisenberry, 1997b). Similarly, Ni *et al.* (1998) found that the leaf epicuticular waxes of different cereal grains were similar and had little effect on the resistance towards the RWA.

Another factor that could influence an aphid's settling behaviour is when it encounters another aphid or a similar obstacle; a 'dummy' aphid. The black bean aphid, *Aphis fabae*, probed more often and remained longer near other aphids than apart from them (Ibbotson & Kennedy, 1951). Prado & Tjallingii (1997) showed that *A. fabae* had beneficial effects when they were placed on leaves that had previously been infested. This indicated the presence of phloem factors that enhances sieve element acceptance by the aphids, although mesophyll and non-vascular phloem tissue factors could not be excluded. This can be considered as host-plant acceptance. In contrast, the bird cherry-oat aphid, *Rhopalosiphum padi*, does not seem to benefit from gregarious living (De Barro, 1992), or from previous infestations (Prado & Tjallingii, 1997). *Rhopalosiphum padi* has been shown to display avoidance behaviour and increased mobility at high population densities due to a communicative odour stimulus (Pettersson *et al.*, 1995).

When the aphid finds a suitable probing site, the labium (which houses the stylets) are placed on the substrate (Miles, 1968). Sheath material is discharged from the tips of the stylets. Analysis of the sheath material of the milkwood bug, *Oncopterus fasciatus*, showed that the proteinaceous stylet sheath consist of approximately 10% phospholipids (Miles, 1960; Miles, 1967). The sheath material gels rapidly as soon as it comes into contact with air or other aqueous media. The precursors of the sheath material occur together with companion molecules that prevent premature gelling. The companion molecules are free sulphhydryl groups and free amino acids. Once the sheath material has been discharged, the amino acids diffuse away and the precursors

come into contact with oxygen, causing hydrogen and disulphide bonds to be formed respectively (Miles, 1964b). This causes the sheath material to gel.

The discharged sheath material gels between the stylets and the end of the labial groove (Miles, 1959b; Miles, 1999). This is known as a flange and forms a structure that is external to the substrate. The stylets are then forced into the plant. It has been hypothesized that the flange serves in securing the tip of the labium to the leaf surface during insertion of the stylets (Saxena, 1963) and also in preventing the stylets from slipping (Pollard, 1973). This could be due to the lipoprotein composition of the flange causing it to adhere to the leaf surface (Miles, 1964b).

Once the RWA stylets have penetrated the leaf surface, the stylets initiate the process of locating the phloem. The RWA feeds from the phloem sap (Fouché *et al.*, 1984).

2.3.2 Location of the food source

Once the aphid stylet has penetrated the epidermis, sheath material continues to be discharged and forms a lining around the stylet which continues along the chosen path. This is known as a stylet sheath. The first observation of a stylet sheath was by Prillieaux (Miles, 1968). It was originally thought that the stylet sheath was due to the reaction of the plant to insect penetration and not from the insect itself. However, an identical structure was found when aphids were allowed to feed on artificial media (Bennett, 1934).

The function of the stylet sheath is debatable. Tjallingii and Hogen Esch (1993) have shown that the stylet sometimes slides between the cell wall and the membrane and do not always follow an accurate intercellular path. During this process the stylet may pierce the plasmalemma and a small amount of watery saliva is discharged (Martin *et al.*, 1997). A small quantity of cell sap is sucked out and the stylet is then withdrawn. The cells that were punctured do not seem to partake in any hypersensitive response of the plant to the aphid. The sheath material has been shown to plug the gap in the cell wall and provide a surface so that repair of the membrane can occur (Tjallingii & Hogen Esch, 1993).

Aphids secrete another kind of saliva that is called the watery saliva. This saliva is water-soluble and does not gel. During the stylet path towards the phloem, the stylet often protrudes from the end of the sheath material during the formation of the stylet sheath (Miles, 1959b). The stylet discharges some watery saliva and this is then ingested together with any liquids surrounding the stylet tip (Campbell & Dreyer, 1990; Tjallingii & Hogen Esch, 1993; Martin *et al.*, 1997). Consequently, aphids can assess the chemical nature of the plant matrix polysaccharide and the cells that have been punctured, as well as determine the acceptability of the host plant by ingesting the discharged watery saliva (Campbell & Dreyer, 1990; Tjallingii & Hogen Esch, 1993).

The watery saliva contains a large number of amino acids that are probably unutilized products that have been absorbed from the phloem sap (Srivastava, 1989). The watery saliva shows strong reducing activity (Miles & Harrewijn, 1991). The pH of the watery saliva was found to be about eight (Miles, 1965).

Pectinases were found in the watery saliva (Adams & McAllan, 1956; 1958). Pectinases (pectinesterase and polygalacturonase) from the greenbug, *Schizaphis graminum*, have been shown to elicit responses in susceptible sorghum plants. These responses were chlorophyll loss and leaf discoloration, similar to that found when the greenbug feeds on susceptible sorghum plants (Ma *et al.*, 1998). It has been hypothesized that the released pectinases may digest the middle lamellar pectin. This facilitates stylet penetration (Dreyer & Campbell, 1987). Tjallingii and Hogen Esch (1993) found that the stylet does not follow a middle lamella path, contradicting Dreyer and Campbell (1987), but in fact follows the secondary walls. Also, stylet penetration seems to go faster than pectin degradation (Cherqui & Tjallingii, 2000). The action of pectinases on pectin also causes the release of pectic fragments, which may be biologically active and elicit plant responses (Ma *et al.*, 1998).

The enzyme amylase has been reported to occur but the validity of these claims is dubious (Miles, 1999). Oxidases are also found in the watery saliva (Miles, 1964a). During plant penetration by an aphid, polyphenols (like catechin) accumulate as a defense reaction to the aphid. Phenoloxidases catalyze toxic phenolics to non-toxic end products (Peng & Miles, 1988). Peroxidases are also reported to occur in the watery saliva of several aphids. This enzyme oxidizes a variety of defensive phytochemicals so that they are detoxified (Miles & Peng, 1989). Both the actions of phenoloxidases and peroxidases prevent the accumulation of products in the plant that will initiate a defense reaction to the aphid.

Several functions for the watery saliva have been proposed. Watery saliva can function as a lubricant to the stylets (Miles, 1999). The aphids can assess the chemical nature of the plant matrix polysaccharide and the cells that have been punctured, as well as determine the

acceptability of the host plant by ingesting the discharged watery saliva (Campbell & Dreyer, 1990; Tjallingii & Hogen Esch, 1993). Aphids have no Malpighian tubules and it has been postulated that the salivary glands assist with excretion (Miles, 1999). The composition of the saliva changes with diet and may even contain organic or inorganic radioisotopes (Lamb *et al.*, 1967; Forrest & Noordink, 1971). Other functions of the watery saliva are dependent on the salivary enzymes and have already been described.

The stylet follows an intercellular path until the phloem is reached (Fouché *et al.*, 1984). The next section will give an account of phloem ingestion.

2.3.3 Ingestion

Once the aphid stylet has entered the vascular bundle (phloem) no more sheath material is secreted. An electrical penetration graph (EPG) monitors aphid activities and the position of the stylet during probing. The EPG allows the probing behaviour of aphids as well as the aphid-plant relationship to be studied (Tjallingii, 1988). From the EPG data it was concluded that in general, aphids make three types of sieve element punctures (Tjallingii, 1990; Tjallingii & Hogen Esch, 1993). Firstly, a brief puncture into the phloem cells which is indistinguishable to punctures made into other cells. This seems to indicate ignorance or no recognition of the phloem cell by the aphid (Tjallingii & Hogen Esch, 1993). Secondly, a puncture into the phloem cell with the continuous discharge of watery saliva which is mixed with the phloem sap. This is known as the phloem salivation phase (E1) (Prado & Tjallingii, 1994). During E1 no saliva is ingested because the food canal within the stylets is filled with fluid (watery saliva). E1 indicates aphid

recognition but no ingestion of the phloem sap (Tjallingii & Hogen Esch, 1993). E1 is often but not always followed by E2. E2 is the phase in which saliva is discharged and mixed with the phloem sap. This watery saliva is then immediately ingested by the RWA and the saliva does not reach the plant tissue. This was proven using viruliferous *Rhopalosiphum padi* individuals. During E2 no virus was inoculated into the plant (Tjallingii, 1988; Prado & Tjallingii, 1994). This mixture of saliva and phloem sap is forced back into the stylets by phloem sap pressure. E2 indicates acceptance of the phloem sap with sap ingestion (Tjallingii & Hogen Esch, 1993). The phloem sap is not always accepted, in which case the aphid withdraws its stylet and probes again.

RWA feeding on resistant wheat and wheatgrass cultivars were found to spend significantly less time ingesting from the phloem compared to RWA on susceptible cultivars. RWA feeding on these resistant cultivars also spend more time in nonphloem ingestion. Kindler *et al.* (1992) suggested that the phloem sap of resistant plants do not provide the necessary structural and chemical cues for phloem acceptance by the RWA. The aphid subsequently turns to nonphloem feeding to survive. The same was observed when the RWA was allowed to feed on resistant and susceptible barley cultivars. Significantly less time was spent feeding on the phloem on the resistant cultivars when compared to the susceptible cultivars. Also, aphids on the resistant cultivars spend more time in nonphloem ingestion (Webster *et al.*, 1993).

RWA feeding on susceptible wheat significantly increased the concentrations of essential amino acids of the phloem, particularly tryptophan and leucine. Infested resistant wheat showed that levels of essential amino acids were slightly decreased (Telang *et al.*, 1999; Sandström *et al.*, 2000). The RWA has endosymbiotic bacteria (*Buchnera* sp.) which overproduce limiting amino acids which benefit their hosts (Douglas, 1988). These bacteria synthesize two essential amino

acids for the RWA, namely tryptophan (Lai *et al.*, 1996) and leucine (Thao *et al.*, 1998). There is a reduction in the number of gene copies of these two amino acids carried by the endosymbiotic bacteria in the RWA (Lai *et al.*, 1994; Thao *et al.*, 1998). Subsequently, a more efficient mechanism for utilizing nitrogen by the RWA has resulted in loss of copies of these genes by *Buchnera*. The RWA manipulates the nutritional quality of the phloem sap of susceptible wheat to improve the quality of its diet and reduces the need for provisioning by the endosymbiont.

2.3.4 Withdrawal of stylets

Once the aphid has completed feeding or has not accepted the phloem sap, the stylets are withdrawn. Withdrawal of the stylets may be completely through the stylet sheath or they may draw back the tips of the stylets for a short distance before the stylet is pushed through the side of the stylet sheath to produce a branch (Miles, 1972). Branched salivary sheaths have been shown to occur in both susceptible and resistant wheat cultivars (Ni & Quisenberry, 1997a). Complete withdrawal of stylets from the plants leaves the stylet sheath behind. The stylet sheath is sealed and filled up with a secretion so that no plant sap can enter (Kinsey & McLean, 1967). The secretion filling the stylet sheath upon withdrawal has been postulated to be watery saliva (Miles, 1959b; Kinsey & McLean, 1967).

RWA on resistant wheat cultivars were found to probe more and for a longer duration compared to aphids on susceptible wheat cultivars (Webster *et al.*, 1993). However, the number and duration of probes by the RWA on the susceptible and resistant wheat and wheatgrass cultivars did not differ significantly (Kindler *et al.*, 1992).

2.4 Methods of curbing RWA damage

Wheat is one of the major staple crops in South Africa (Marasas, 1999). The RWA can cause an average of 60% loss to yield (Hewitt, 1988). Four methods have been used to reduce the economic impact and the damage that the aphid causes:

2.4.1 Cultural practices

The RWA survives the summer season by living on alternate hosts, for example, rescue grasses (Kindler & Springer, 1989). Avoidance in planting these alternate hosts (*e.g.* barley) earlier than the planting of wheat will lead to a decrease in the numbers of the RWA. This also deprives the aphid of its refuge (Walters *et al.*, 1980). These refuges are the source of RWA infestations into wheat fields.

The choice of planting date should be reviewed. Walters *et al.* (1980) suggested that crops should not be planted before May. Also, wheat that is densely planted and well fertilized is not susceptible to heavy aphid infestations.

Cultural control of the RWA was largely practiced when the RWA was first discovered in South Africa. There were no RWA resistant wheat cultivars and little information was available on insecticide usage against this aphid (Du Toit & Walters, 1984).

2.4.2 Insecticides

RWA susceptible plants exhibit leaf rolling that provides an optimum environment that protects the RWA from contact insecticides (Miller *et al.*, 1994). RWA are also found in the axils of leaves and within the leaf whorl, which also restricts the action of contact insecticides (Walters *et al.*, 1980). Subsequently, systemic insecticides have proven more successful in controlling the RWA (Robinson, 1992).

The irresponsible use of insecticides is harmful to the environment and can destroy the aphid's natural enemies. The use of insecticides is also an expensive practice that increases production cost. Insecticide treated wheat may be unacceptable for export to Europe. Continued injudicial use of insecticides may accelerate the development of insecticide resistance by the aphid (Wolff *et al.*, 1994). More environmentally friendly methods of combating RWA infestations are desirable.

2.4.3 Biological control

The RWA is an introduced insect pest in South Africa, where its native natural enemies are absent. Consequently, the RWA has flourished on susceptible wheat.

Biological control agents of aphids can reduce the population levels of aphids. In South Africa, seven indigenous species of parasitic wasps and two species of predatory flies have been found to attack the RWA (Hayes, 1998). These natural enemies are, however, unable to prevent RWA

populations from causing severe damage on susceptible wheat (Aalbersberg *et al.*, 1988). Several natural enemies have been introduced into South Africa to combat the RWA. One of these is a parasitic wasp, *Aphelinus hordei*, introduced from the Ukraine in 1991 (Prinsloo, 1998). Female wasps lay their eggs inside the aphid and the larvae which hatch feed on the aphid. In field trials during 1996, parasitism of up to 72% was recorded (Hayes, 1998).

Other reports have shown that parasitism of the RWA also decreases aphid populations on susceptible wheatgrass (Reed *et al.*, 1992). However, susceptible wheatgrass that displayed leaf rolling had a decreased incidence of parasitism of the RWA because the RWA could hide from the parasitoid (Miller *et al.*, 1994). Farid *et al.* (1998) showed that *Diaretiella rapae* females (hymenopterous parasitoids) that emerged from RWAs that were maintained on resistant wheat, had a longer life span. RWAs fed on resistant wheat had no adverse effects on the parasitoid, indicating the compatibility of the resistant cultivar and the parasitoid.

The RWA lives and feeds in rolled leaves of susceptible plants and this provides some protection to the RWA against predators (Miller *et al.*, 1994). To combat this, the use of disease-causing fungi as a possible biological control agent against the RWA, have been attempted (Feng & Johnson, 1991). *Beauveria bassiana* has been shown to increase aphid mortality but has no significant effects on fecundity. Also, RWA nymphs may become infected when they come into contact with dead sporulating adults (Wang & Knudsen, 1993).

In South Africa, pathogenic fungi have been observed to attack the RWA, but only during the warm, moist summer months. The RWA is important only during the winter months when wheat is planted (Walters *et al.*, 1980). Six species of entomopathogenic fungi have been recorded in

South Africa. These include *Beauveria bassiana*, *Pandora neoaphidis*, *Conidiobolus obscurus*, *Conidiobolus thromboides* and *Entomophthora planchoniana* (Hayes, 1998; Hatting *et al.*, 2000). RWAs were shown to have higher susceptibility to *P. neoaphidis* (Hatting *et al.*, 2000).

Biological control agents are however, affected by environmental conditions. Introduced predators and parasitoids may not become active early enough to exert control over the RWA, as they do not have synchronized life cycles.

2.4.4 Planting of resistant cultivars

When the RWA was first discovered in South Africa on wheat during 1978 no wheat cultivars displayed any resistance (Walters *et al.*, 1980) and large scale insecticide applications were made annually. Emphasis was placed on identifying resistant *Triticum* genotypes from the RWA native countries (Du Toit, 1987). Attempts were then made to transfer this resistance to locally adapted cultivars by traditional breeding methods (Du Toit, 1989).

From the resistant wheat cultivars that were originally developed, 'Tugela *DnI*' was the first resistant wheat cultivar to be released for commercial production in the world. 'Tugela', a local susceptible winter wheat cultivar, was crossed to PI 137739 (also known as SA 1684), a resistant wheat cultivar originating from Iran (Du Toit, 1987; 1989). The F₁ progeny were then backcrossed five times to 'Tugela'. The result was 'Tugela *DnI*', a hard red, semi-dwarf bread wheat cultivar that can be cultivated under dryland conditions in the summer rainfall region (Small Grain Institute (SGI), Bethlehem). Resistance reactions showed that the resistance of

'Tugela *DnI*' is controlled by a single dominant gene (*DnI*) and that this gene is inherited independently to other RWA resistance genes (Du Toit, 1989).

The development and use of resistant cultivars may represent the most effective way to overcome RWA infestations of cereals. Resistant cultivars are environmentally safe and economical in comparison to the use of insecticides or biological control (Budak *et al.*, 1999).

Possible sources of resistance that have been described are antibiosis, antixenosis (nonpreference) and tolerance.

2.4.4.1 Antibiosis

Painter (1958) first coined the terms antibiosis, nonpreference and tolerance. The term antibiosis is defined as the ability of resistant plants to adversely affect the biology of an insect. Plants that express antibiotic resistance to insects are obviously less suitable hosts than susceptible cultivars (Mowry, 1994).

The most common category of resistance in wheat is antibiosis (Du Toit, 1987, 1989; Unger & Quisenberry, 1997). Aphids feeding on plants exhibiting antibiosis (resistant plants) experience decreased longevity, delayed development, decreased fecundity and an increase in restlessness (Painter, 1958; Scott *et al.*, 1991; Baker *et al.*, 1992; Kindler *et al.*, 1992; Smith *et al.*, 1992). The most typical parameter that is used to assess antibiosis in wheat plants is RWA fecundity. This is assessed measuring the rate of nymphal production, the length of the nymphipositional

period (the period that nymphs are produced) and adult life span (Smith *et al.*, 1992; Unger & Quisenberry, 1997).

Very few wheat cultivars are found that display all three categories of resistance (Unger & Quisenberry, 1997). PI 137739 displays both antibiosis and antixenosis (Du Toit, 1987); low levels of tolerance to the RWA was found by Smith *et al.* (1992). Antibiosis causes selective pressure on the insect (Tolmay *et al.*, 1999). This can result in the insect developing resistance to the plant exhibiting antibiosis (Gould, 1998). Tolerance, which does not impose selection pressure on the insect, can be used in conjunction with other sources of resistance, to prevent or delay adaptation by the insect (Haile *et al.*, 1999).

Antibiotic resistance to the RWA seems to involve different and independent genes (Castro *et al.*, 2001). Subsequently, the genotypes carrying these genes need to be selected to broaden the genetic base from which to choose resistance genes in a breeding program.

2.4.4.2 Antixenosis (nonpreference)

The term antixenosis is defined as the nonpreference of plants for insect oviposition, shelter or food. This is primarily due to the lack of certain qualities of the plant (Painter, 1958).

Antixenosis is the inability of a plant to serve as a host for a pest. It is caused by physical or chemical plant factors that repel or deter insects from feeding and ovipositing on the plant (Tolmay *et al.*, 1999). Nicol *et al.* (1992) showed that there were significant correlations between

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b 15413500

aphid nonpreference (plant resistance) and the concentration of 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA). DIMBOA is a hydroxamic acid that has deleterious effects on insects feeding on cereals (Mayoral *et al.*, 1996).

Antixenosis is measured by planting seeds of different cultivars randomly in a circle and releasing the RWA in the center. The distribution of the aphid is determined after a certain duration and the aphids preference is subsequently determined (Tolmay *et al.*, 1999). Some reports have indicated a great deal of variability in this approach (Webster *et al.*, 1987; 1991). Antixenosis seems to be the result of the action of multiple genes found on the group 7 chromosomes (Castro *et al.*, 2001).

As with antibiosis, antixenosis also causes selective pressure, but to a lesser degree than antibiosis. This can result in the aphid developing resistance to the plant exhibiting antixenosis. Subsequently, care should be taken when exposing the RWA to plants exhibiting only antixenosis for long periods of time.

2.4.4.3 Tolerance

Plants are tolerant if they survive under levels of infestation that would kill or severely injure susceptible plants (Painter, 1958). A resistant plant that displays tolerance has the ability to withstand infestation while still supporting insect populations that would severely damage susceptible plants (Scott *et al.*, 1991).

Known components of tolerance include plant vigour, compensatory growth, wound healing and changes in photosynthetic partitioning (Tolmay *et al.*, 1999). This mechanism of resistance is determined by measuring plant height, plant dry mass, plant fresh weight and the damage rating of the plants infested with the RWA (Du Toit, 1988; Unger & Quisenberry, 1997; Tolmay *et al.*, 1999).

The use of plant tolerance as a resistance mechanism against the RWA has been emphasized more than other systems (Haile *et al.*, 1999). Baker *et al.* (1992) found that moderate levels of tolerance measured in the greenhouse often correlates to a tolerance under field conditions. The genetic basis of the three resistance mechanisms (antibiosis, antixenosis and tolerance) show that multiple genes appear to govern resistance towards the RWA and that many of these resistant genes seem to be independent (Castro *et al.*, 2001). Pyramiding of genes enhances the genetic basis of resistance to the RWA and makes it more difficult for the RWA to overcome the resistance posed by the plant.

2.5 RWA induced protein alterations

The RWA feeds on phloem sap via a stylet that follows an intercellular path (Fouché *et al.*, 1984). Little information is available on the response of the plant to RWA feeding. Evidence suggests that plants react in a similar fashion to RWA infestation as defense reactions that are caused by pathogen attack, wounding or herbivorous insects (Givovich & Niemeyer, 1996; Botha

et al., 1998; Van der Westhuizen *et al.*, 1998). The objectives are to determine if RWA inducible responses are related to the resistance that plants possess.

RWA feeding on barley showed that on a susceptible 'Morex' line, a complex of proteins (≈ 22 to 24 kDa) disappeared from the protein profile although these had previously been present in the uninfested control. This same protein complex shifted its isoelectric point (toward the basic end) when the resistant barley line (PI 366450) was infested with the RWA (Porter, 1992). Using two-dimensional gel electrophoresis, the protein complex was found to be 23 kDa (Miller *et al.*, 1994). Porter & Webster (2000) found that in spring wheat there is a 24 kDa complex that was inhibited in a susceptible line ('Pavon') but this complex persisted in the resistant line (PI 140207) during RWA infestation.

PI 137739 (SA 1684) and other plant derivatives possessing the *Dn1* gene have been studied in terms of inducible changes as a result of RWA feeding. Rafi *et al.* (1996) showed an induction of three polypeptides ($\approx 32, 33$ and 35 kDa) upon RWA infestation in PI 137739 (RWA resistant) but not in a susceptible wheat cultivar ('Stephens'). It was suggested that these induced proteins may play a role in plant defense, involvement in the antibiosis displayed by PI 137739, interaction in the reproduction of the RWA or in senescence. Three proteins were also found to be altered in both the susceptible and resistant cultivars. These proteins showed a reduced expression and could be due to the RWA or to wounding by the aphid (Rafi *et al.*, 1996).

Protein profiles of the intercellular washing fluid (IWF) from 'Tugela' and 'Tugela *Dn1*' (these are near-isogenic lines) showed the induction of four complexes of proteins (28-33, 22-24, 18.5-

19.5 and 15.5-17 kDa) upon RWA infestation of the resistant cultivar. Western blots showed that these complexes consists of β -1,3-glucanase, chitinase and PR-S proteins (related to enzymes that possess antifungal activities). Not all proteins were identified (Van der Westhuizen & Pretorius, 1996). The RWA probes intercellularly and these induced proteins might play a role in the resistance that the RWA encounters when feeding on these resistant lines. The RWA has been shown to feed less from the phloem on resistant cultivars and turns to nonphloem feeding to survive (Kindler *et al.*, 1992). Here the RWA might encounter some of these induced proteins which possibly adversely affects the RWA.

When comparing 'Tugela' (RWA susceptible) and its near isogenic line 'Tugela *Dn1*' (RWA resistant), there was a reduction in the water soluble protein content of the third leaves after RWA infestation (Van der Westhuizen & Pretorius, 1995). RWA infestation of 'Tugela *Dn1*' caused an induction of the enzyme β -1,3-glucanase, which was not found for 'Tugela' (Van der Westhuizen *et al.*, 1998). Similar results were found for the enzyme chitinase (Botha *et al.*, 1998). The role of these enzymes in the defense of the plant to the RWA is not clear. One hypothesis is that their action releases oligosaccharides which triggers the defence reactions of the plant, similar to the reaction of the plant to hyphal penetration (Dreyer & Campbell, 1987).

Clearly, more investigations into the exact nature and mechanisms of the induced proteins are necessary to understand their role in the resistance encountered when the RWA feeds on a resistant plant.

2.6 Conclusion

Since the RWA was discovered in South Africa, it has become an important pest on wheat and numerous control methods have been investigated. The use of insecticides has not proven to be cost effective. Resistant plants have been developed and to date the RWA has not overcome this resistance. However, the possibility always exists that this could happen. Understanding the exact mechanism of resistance that these plants pose would help solve this problem if it does arise. The following chapters help in understanding the resistance that the plants possess and how the RWA responds to the resistance of the plants.

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