The potential of wheat, maize, lucerne, and soybean as plant borders to reduce aphid-transmitted virus incidence in seed potatoes

By

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DECLARATION

I, the undersigned, hereby declare that the dissertation submitted for the degree *Magister Scientiae* to the University of Pretoria contains my own independent work and has not been submitted for any degree at any other university.

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Signature

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Date

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Summary

Crop borders have the potential to reduce transmission of non-persistent aphid-borne viruses provided a virus non-host is used as a border plant. Alatae (winged aphids) landing in these crop borders purge their mouthparts of the virus by initial probing behaviour on the virus non-host plant before moving into the field proper. The plant species used affects aphid landing because aphids respond to visual and olfactory cues emitted by their host plants. In addition, crop borders could enhance within-field diversification of agro-ecosystems, thereby increasing the number of food sources available to alatae migrating into potato fields.

The objective of the present study was to determine preference of aphids for selected agricultural crops to identify a potential border crop that could be used as a trap crop as well as a virus sink. To evaluate the potential of lucerne, maize, soybean and wheat as border plants for potato fields, a semi-field trial was undertaken at the University of Pretoria Experimental Farm, Gauteng, South Africa. The four crops were chosen based on discussions with seed potato producers. Aphid abundance, alatae landing rates and aphid species assemblages were compared between the four crops and potato using different collecting methods (leaf counts, sweep-netting and green bucket traps) to eliminate any bias caused by sampling methods. In addition, species overlap and composition of the alatae were compared between a heterogeneous planting in Pretoria and a homogeneous planting in Christiana, western Free State, South Africa. The aim was to determine whether it would be possible to use the plant(s) identified as potential border crops in the semi-field trial in Pretoria as a border crop in the seed potato production region in Christiana.

Results from different sampling methods regarding species composition and abundance on different crops in Pretoria varied according to the method used. Therefore, more than one method should be used when sampling aphids to avoid bias. According to the green bucket trap catches, aphids alighted more frequently on crops they colonized. This suggests that alatae have the ability to select their preferred host plant, if available within a habitat patch, in the pre-alighting phase. Overall, aphid species composition for colonizing and non-colonizing species on maize and wheat was more similar to potato than lucerne and soybean. Based on results of all three methods combined, maize and wheat were identified as the two crops with the highest potential to be used as crop border plants.

Similarity of aphid assemblages between Pretoria and Christiana, based on species composition and abundance, was relatively low. However, comparing presence/absence data, species overlap between the two regions was relatively high, suggesting most of the variation between the two regions was mainly due to differences in aphid abundance. Therefore, maize and wheat could be planted as trap border crops in Christiana. In addition, most aphids landing in potato fields in Christiana do not colonize potato. The most typifying species in this region have been recorded on Poaceae and are vectors of PVY, the most prevalent and important of the non-persistently transmitted viruses in South Africa and other potato-growing regions throughout the world.

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Chapter 1

General introduction

1.1 Aphid-transmitted potato viruses

More than 25 viruses are known to infect potato plants. Examples are *Potato leaf roll virus* (PLRV), *Potato virus A* (PVA), *Potato virus M* (PVM), *Potato virus S* (PVS), *Potato virus Y* (PVY) and *Potato acuba mosaic virus* (PAMV) (Salazar, 1996). Of these PLRV and PVY are the two most economically important viruses in many potato-growing regions globally (Ragsdale *et al*., 2001). Both viruses are transmitted by aphid vectors but differ in their mode of transmission. PLRV is a persistently (circulative virus) and PVY is a non-persistently (stylet-borne) transmitted virus.

Persistently transmitted viruses are acquired when insect vectors feed on phloem sap of infected plants. They pass through the gustatory system of vectors and have a latency or incubation period before they can be transmitted. Only specific vectors can transmit this type of virus (Salazar, 1996; Katis *et al*., 2007). Non-persistently transmitted viruses, on the other hand, can be acquired and transmitted in less than 5 minutes. Brief probes with the stylets into the epidermal layer of leaves are sufficient to acquire this type of virus. The virus particles adhere to the mouthparts of insect vectors, and there is no latent period. The specificity between virus and vector is not marked and this type of virus can be transmitted, in the case of non-persistently transmitted potato viruses, by many aphid species. It is important for the control of non-persistently transmitted viruses that they do not persist in the vector and transmission ability is lost or greatly reduced when vectors feed on virus non-host plants (Nault, 1997).

Crop borders have been shown to be an effective management tool in reducing the spread of non-persistently aphid-transmitted viruses as the virus does not persist in vectors unlike persistently transmitted viruses (Hooks & Fereres, 2006). Because of the prevalence and importance of PVY in many potato-growing regions worldwide, the present study uses PVY as a model in selecting crop border plants for potato fields.

1.2 *Potato virus Y* (PVY)

PVY is of great concern to seed potato growers globally. Infection of seed potatoes (potato tubers) with PVY can cause yield losses ranging from 10 to 100 % due to degeneration of the seed stock (Radcliffe, 1982). PVY is a *Potyvirus* and belongs to the family Potyviridae (Brunt, 2001). World-wide, plant species belonging to more than 14 different families have been identified as hosts of PVY (Brunt, 2001; Chatzivassiliou *et al*., 2004). Hosts include a range of solanaceous crops and weeds. Several strains of PVY have been identified which vary in the symptoms they cause in potato (Blanco-Urguiti *et al*., 1998). For example, PVY^{O} (ordinary or common strain) causes severe mosaic, leaf drop and stem necrosis. The symptoms caused by PVY^{N} (tobacco veinal necrosis strain) are not as severe as in PVY^{O} and can be absent in some potato cultivars but include vein necrosis in tobacco (Blanco-Urguiti *et al*., 1998. Symptoms of PVY^{NTN} (potato tuber necrotic ringspot disease) are much more severe than those caused by any of the other strains and include severe chlorotic mosaic, leaf-drop, severe ring-spot necrosis in tubers and early death of plants (Singh *et al*., 1998).

PVY can be transmitted through primary infection (current season) or secondary infection (planting of tubers from mother plants infected in the previous season). Seed potato growers are more affected by primary infection than ware potato producers. Primary infection has little effect on yield but reduces the quality of the seed stock. Because tubers of infected plants carry PVY, secondary infection leads to reduced tuber size causing considerable yield loss. It is, therefore, important to use only healthy tubers as seed (Hane & Humm, 1999). Seed certification programmes have been developed to monitor PVY infection in seed potatoes. If the percentage of virus infection in a particular seed stock exceeds tolerance levels (0-1%), the seed will be moved to lower class or, in severe cases, will not be sold as seed potatoes (Ragsdale *et al*., 2001).

1.3 Virus transmission characteristics

Transmission of PVY can occur mechanically, through grafting and by aphids in a non-persistent manner. The main form of PVY transmission in the field is through aphid vectors, and more than 50 species are able to transmit PVY (Ragsdale *et al*., 2001). Aphid vectors obtain and transmit PVY through initial probing, i.e. insertion of the stylets into the epidermal layer of a leaf, before feeding on the phloem sap commences. The virus particles do not pass through the digestive tract of the aphid but adhere to the mouthparts, decreasing transmission time considerably. There is no latent period, thus virus transmission can occur immediately after aphid vectors acquire PVY; transmission can occur in less than 60 seconds. The virus does not persist or replicate in the vector. After acquisition and subsequent feeding, vectors lose their ability to transmit PVY and will only be virulifirous for up to 72 hours after acquisition (Swenson, 1968; Nault *et al*., 1997). Therefore, aphid biology and host plant selection behaviour play a key role in virus transmission.

Aphids are very successful in spreading diseases in plants due to their cyclical parthenogenesis (asexual reproduction) enabling them to have several generations per season, polymorphism (occurrence of different morphs within a species), and highly dispersive host-finding behaviour (Blackman, 1976; Dixon, 1977,1998). Factors such as alatae (winged aphids) dispersal patterns, the likelihood of alatae alighting on non-host plants being the same as for host plants, and the intensity and duration of aphid migrations contribute to the success of aphids in spreading non-persistent viruses to crops. These attributes facilitate the transmission of non-persistent viruses to crops that do not fall within the host range of vector species (Swenson, 1968). Alatae are capable of migration flight for long periods dispersing over great distances of more than 100 km with prevailing wind currents and are thus responsible for introducing the virus into the crop from other virus sources, such as volunteer potatoes, other agricultural crops and weeds from within and outside the region (Daiber & Schöll, 1959; Daiber 1965; Radcliffe, 1982; Loxdale *et al*., 1993). Apterae (wingless aphids) play a minor role in virus spread because they do not generally move from their host plant (Ragsdale *et al*., 2001).

Management of PVY is aimed at controlling the vector and source of inoculum and can be preventative (reduction of virus inoculum) or therapeutic (vector control). The main approach in controlling aphid populations on seed potatoes and thus the spread of PVY is with insecticides. Although effective in reducing aphid populations on potato crops, aphids are able to transmit PVY before being immobilized by insecticides (Radcliffe, 1982). Seed potato growers have been advised to follow good cultural practices by removing virus inoculum (rouging) and growing potatoes in isolation to reduce virus incidence (Caldiz *et al*., 2002; Radcliffe & Ragsdale, 2002). These practices currently form the basis of seed certification programmes. To improve PVY management, other control strategies should be implemented in combination with the existing management programme effectively to control the spread of PVY (Radcliffe & Ragsdale, 2002).

One such possible control strategy is the use of plant borders. This usually entails the planting of a plant other than potato around the border of fields. Alatae migrating into fields have been reported to respond to the contrast in colour at the edge of the fields formed by the green of the crop and the fallow ground, causing aphids to land more frequently at edges (DiFonzo *et al*., 1996). After landing on plants, aphids evaluate plants by probing leaves (Powell & Hardie, 2000). This causes aphids to purge their mouthparts of non-persistently transmitted viruses before moving into the main crop (Fereres, 2000). By selecting a plant that is a virus non-host and preferred by aphids to potatoes, the border plant can act as a virus sink, attracting aphids and thus decreasing non-persistently transmitted virus incidence considerably (DiFonzo *et al*., 1996; Hooks & Fereres, 2000). Selecting an agricultural crop as a border plant can be compatible with current production practices, resulting in a relatively simple control method. Therefore, no additional equipment would be needed provided that the crop selected is part of the planting regime in the area (Ragsdale *et al*., 2001).

1.4 Research objectives and thesis outline

The first aim of this study was to determine the preference of aphids for specific agricultural crops in order to identify a potential crop border plant. Four crops, lucerne, maize, wheat and soybean, were planted in a semi-field trial. The field component of the study was carried out at the University of Pretoria Experimental Farm, Gauteng, South Africa. The semi-field trial could not be undertaken in a seed potato-production region in South Africa. Therefore, the second aim was to compare aphid species composition recorded from the crops in Pretoria to aphid species composition recorded from potato fields in a field trial undertaken in the seed potato production region of Christiana, western Free State, South Africa. The objective was to determine whether the crop(s) identified as suitable border plants from the semi-field trial could be used in the Christiana region, i.e. whether findings from one region would be applicable to another region.

The thesis chapters are written in the form of research papers. Therefore, there is some overlap between chapters with regard to parts of the text. Chapter 2 gives a brief overview of aphid classification and the morphological features used to distinguish between aphid species in the current study, aphid biology and host plant selection behaviour. Different strategies proposed to manage PVY spread are discussed. Chapter 3 investigates the first aim of the study and deals with aphid host plant selection behaviour. In this section the usefulness of different aphid collection methods in evaluating aphid host plant-selection behaviour is compared. Three methods were used to sample aphids during the semi-field trial in Pretoria. Chapter 4 compares aphid species assemblages and compositions of the two different regions. The potential of implementing management strategies in a seed potato agro-ecosystem inferred from an experimental study conducted in a different region with differing landscapes is discussed. Chapter 5 gives a general discussion and conclusion of the results presented in this study and future research possibilities are discussed.

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Chapter 2

Aphid systematics, morphology, biology and control

2.1 The Aphidiodea

Aphids (Hemiptera: Aphidiodea) are small (1.5-3 mm) soft bodied insects with piercing sucking mouthparts. The group is responsible for considerable yield losses in many agricultural crops. Aphids occur on ornamental plants as well as trees and can be problematic in forestry as well as agriculture (Millar, 1990). Of the approximate 4,700 aphid species occurring throughout the world, 136 species are found in South Africa. Only a small number, about 100 species, have exploited the agricultural environment to the extent of becoming well known pests. More than 30 of these occur in South Africa (Annecke & Moran, 1982; Millar, 1990; Blackman & Eastop, 2007). The primary concern with aphids is their role as virus vectors of agricultural crops. However, high aphid numbers on crops can result in considerable direct yield losses (Swenson, 1968, Radcliffe, 1982).

Aphid identification poses many pitfalls due to the high variation observed in their morphological features as well as the effect of environmental factors and host plant quality on their phenotype. Therefore, identifications based on single morphological characteristics may be misleading and several characteristics from more than one individual should be examined where possible (Millar, 1990; Blackman & Eastop, 2007; Poulios *et al.*, 2007). The intraspecific variation found in morphological features of the Aphidoidea is larger than in any other insect group. Within species variation, such as differences in size and colour, may occur within a season (Wool & Hales, 1997; Cisneros & Godfrey, 2001; Nevo & Coll, 2001). Environmental conditions, such as temperature, can affect body size, pigmentation, number of offspring and allometry during development. Host plant nutrition affects the size of the offspring. This can lead to the production of dwarfed individuals over several generations on a poor quality host plant. The opposite is true when host plant quality is high (Nevo & Coll, 2001; Blackman & Eastop, 2007). For example, Nevo & Coll (2001) correlated body size of *Aphis gossypii* (Glover) with nitrogen levels of cotton plants. The use of morphometric features to distinguish between closely related species should thus be done with caution (Moran *et al.*, 1993; Kocourek *et al.*, 1994; Blackman & Eastop, 2007).

A second caveat contributing to the wide range in variation is the effect of photoperiod, nutrition and crowding on the phenotypic expression of individual colonies within a species (Vaz Nunes & Hardie, 1992; Blackman & Eastop, 2000; Müller *et al.*, 2001). Aphids are able to reproduce sexually, overwintering in the egg stage, as well as asexually (parthenogenetically). The sexual morphs (winged) are mainly found in the autumn months and are associated with a decrease in temperature and day length, while the parthenogenetic females (winged and unwinged) can be found throughout the year depending on the species and environmental conditions (Dixon, 1977). Alatae (winged) and apterae (unwinged) morphs differ to a great extent in their morphology and separate keys are needed to identify the different morphs (Hardie, 1980; Millar, 1990). However, it is possible for apterous morphs to display alatiform characteristics and *vice versa*. A good understanding of aphid biology and polymorphism is thus needed when examining a field collected sample of aphids for identification purposes. A problem can occur when all individuals examined are from a single clone. Because aphids reproduce parthenogenetically, an entire colony can express a morphological abnormality when founded by a single female. This has resulted in species being erroneously described as new species in the past (Millar, 1990; Blackman & Eastop 2000; Blackman & Eastop 2007).

2.2 Aphid systematics

There exists a lot of controversy amongst taxonomists on the classification of aphids on the family level (Ilharco & van Harten, 1987; Millar, 1990; Blackman & Eastop, 2000). The present study followed the classification used by Millar (1990) and Blackman & Eastop (2000). Aphids are all grouped in a single superfamily, the Aphidoidea, which is subdivided into the three families Adelgidae, Phylloxeridae and Aphididae. The superfamily Aphidoidea belongs to the series Sternorrhyncha in the order Hemiptera along with scale insects, psyllids and whiteflies. The most characteristic feature of the Sternorrhyncha is the position of the rostrum, which has its base between the forecoxae and is placed in a groove along the ventral side of the body in resting position. The Sternorrhyncha also have relatively well developed antennae and tarsi with one or two segments (Blackman & Eastop, 2000).

The Adelgidae and Phylloxeridae are distinctly different from the Aphididae and retain some primitive features such as the absence of viviparity and siphunculi. Some taxonomists prefer to place these groups in a separate superfamily, the Phylloxeroidea. The remaining major groups of aphids are further placed into families (Lachnidae, Aphididae etc.) within the superfamily Aphidoidea. The system used in this study places these groups into subfamilies (Lachninae, Aphidinae etc.), in the family Aphididae (Ilharco & van Harten 1987; Blackman & Eastop, 2000). The full classification system used in the present study as set out by Millar (1990) is given in Appendix A.

2.3 Aphid morphology and key characteristics

The description of aphid morphology given here is rather superficial as the present study is not of a taxonomic nature. However, the study could not be performed without identifying the aphids collected from the field experiments because aphid species differ in their host plant range and ability to transmit viruses (Millar & Dürr, 1985; Ragsdale *et al*., 2001). Therefore a good understanding of aphid taxonomy and diagnostic features was imperitive in completing the present study. This brief overview will concentrate on the winged and wingless parthenogenetic females as aphid taxonomy is based on the adult viviparous female (Fig. 2.1) and only parthenogenetic forms were collected throughout the study (Millar, 1990).

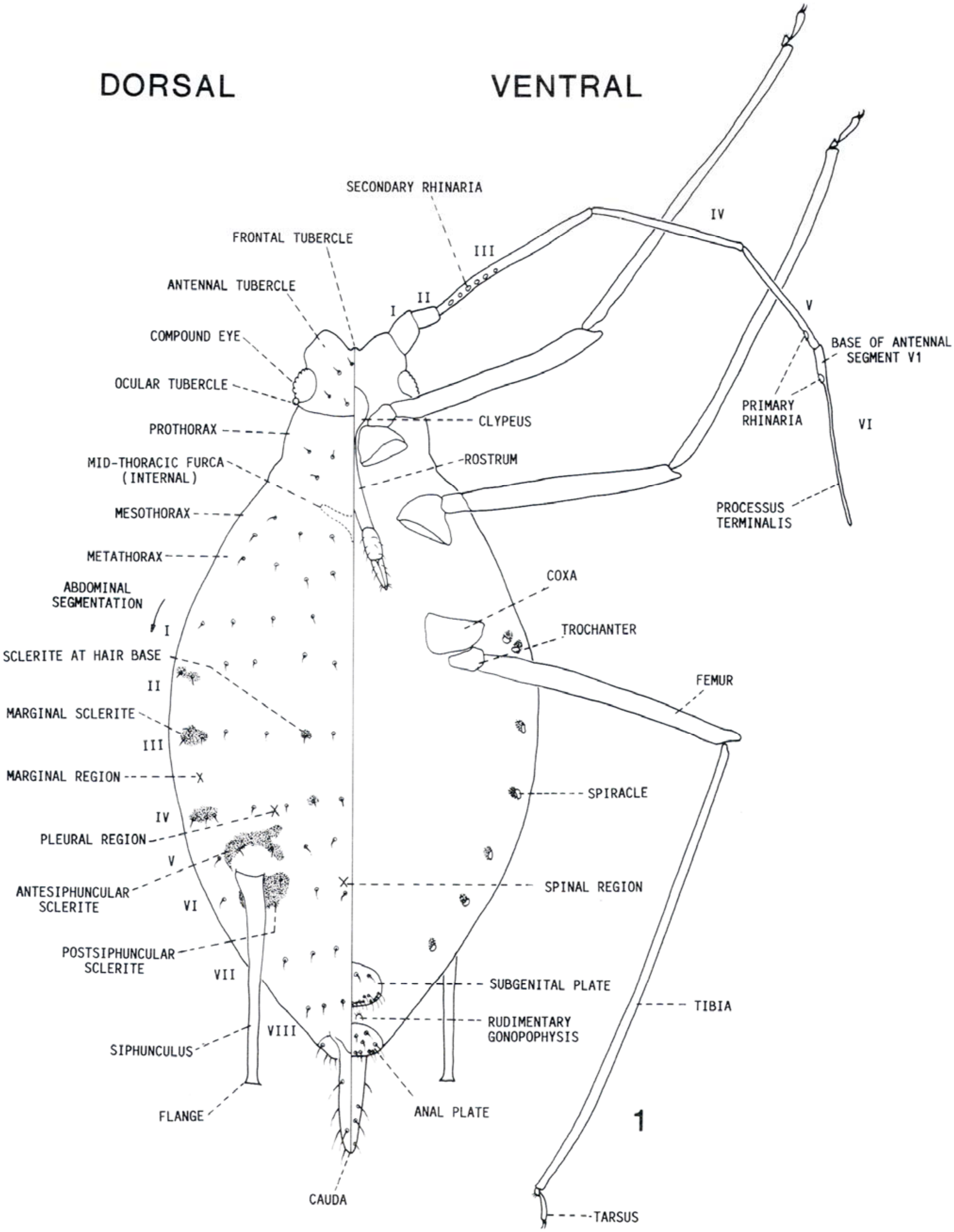

Fig. 2.1. Morphological features of an apterous female (from Millar, 1990).

2.3.1 Head

The latero-frontal part of the head has a characteristic form in many aphids when viewed dorsally, especially in the Macrosiphini (Millar, 1990). Often the antennal bases are more or less developed and extended upwards or forwards to form antennal tubercles or frontal tubercles. Frequently the front of the head takes on a w shaped appearance due to a median frontal prominence between the antennal tubercles. The inner margin of the antennal tubercles can be diverging, parallel or converging which may be smooth or roughened with spinules (Fig. 2.2). This characteristic is more prominent in apterae than in alatae and is best seen in specimens preserved in alcohol as slide mounting may obscure this characteristic when the head is tilted or bent upwards (Blackman & Eastop, 2000).

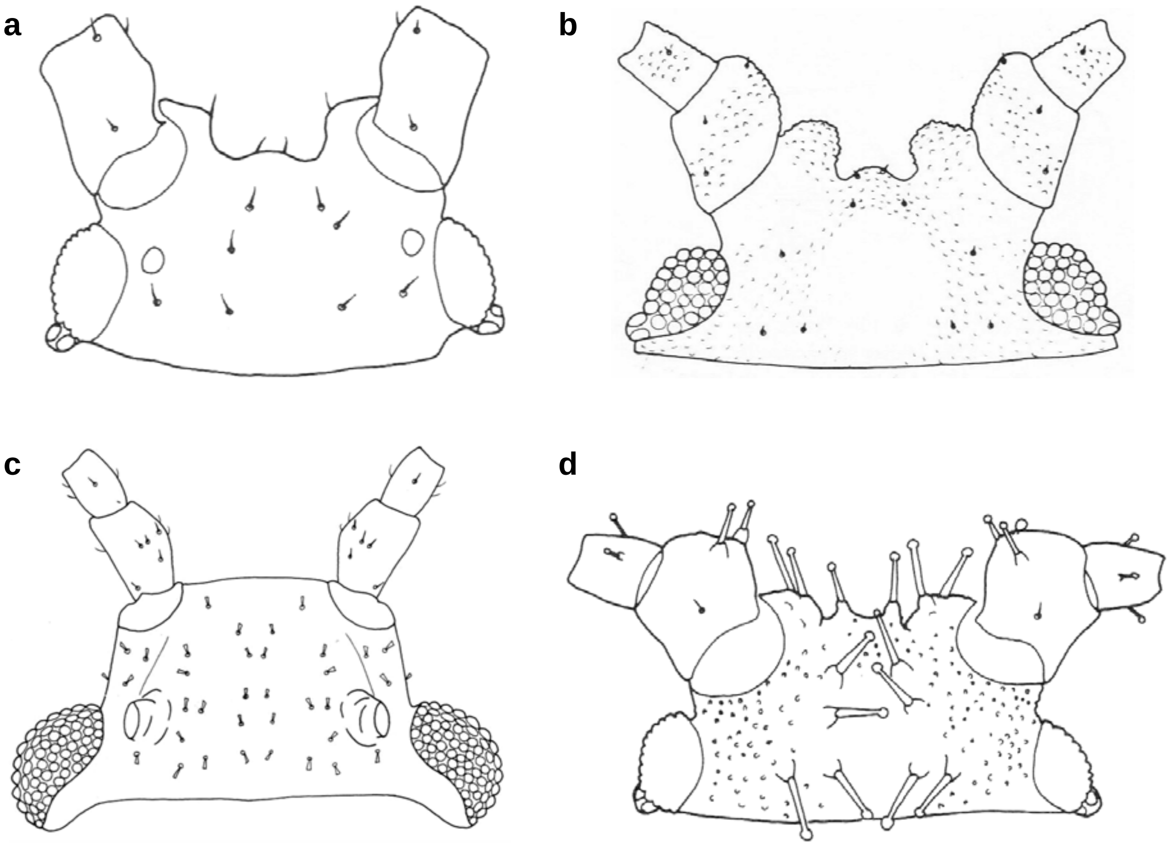

Fig. 2.2. Antennal tubercles of aphids. Well developed, divergent (a), well developed, convergent (b), weakly developed (c) and well developed frontal projection (d) (from Millar, 1990).

Other characteristics of the head used as diagnostic features are the length of hairs on the frons or vertex. Three types of eyes are distinguished among aphids, compound, multi-faceted or comprising of three facets (triommatidium). Adult alatae always have compound eyes with three ocelli, apterae however lack ocelli, unless they are alatiform. On the posterior margin of the compound eye an ocular tubercle (three faceted process) is usually present (Fig. 2.3). The visibility of the ocular tubercle in dorsal view is sometimes used as a diagnostic feature as it is not visible in some species (Millar, 1990).

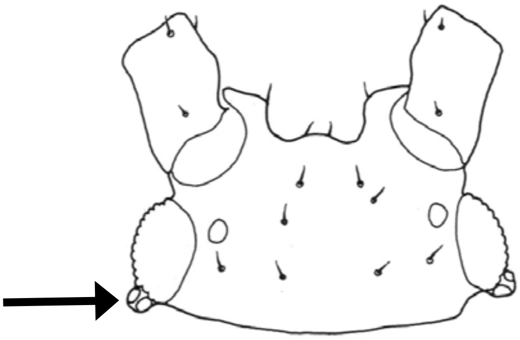

Fig. 2.3. Ocular tubercle (triomatidia) in dorsal view (from Millar, 1990).

The length of the last rostral segment (segment V and IV fused together) (Fig. 2.4) is usually used in comparison to the length of the second tarsal segment of the hind leg (Fig 2.5). This characteristic is more accurately measured in slide mounted specimens (Blackman & Eastop, 2000).

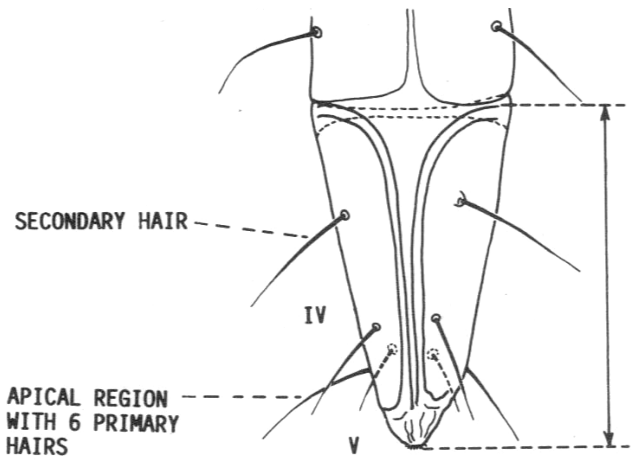

Fig. 2.4. Ultimate rostral segment (from Millar, 1990).

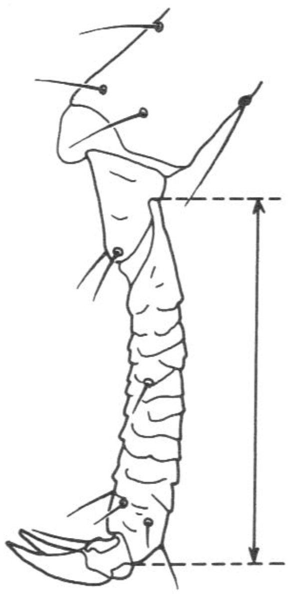

Fig. 2.5. Second tarsal segment (from Millar, 1990).

2.3.2 Antennae

Aphid antennae are mostly six-segmented, but can be four- or five-segmented. Segments I and II are referred to as the scape and pedicel, respectively, and are considerably shorter than the remaining segments, termed the flagellum. The last antennal segment consist of two parts; the wider basal part and the thin terminal process. They contain a large primary rhinaria (olfactory placoid sensillum) between them and sometimes a group of small accessory sensoria next to it (Fig. 2.1). The length of the basal part relative to the length of the terminal process is often used as a diagnostic feature along with the relative proportions of the antennal segments (Ilharco & van Harten, 1987; Millar, 1990).

Secondary rhinaria, when present are usually smaller and can be of various characteristic shapes, i.e. oval, rounded, transversely elongate, or very elongate and ring like (Fig. 2.6). Other antennal features used in aphid identification are the length of the antenna relative to body size and the number and distribution of secondary rhinaria. Alatae aphids generally have secondary rhinaria on at least the third antennal segment. In the apterae of the same species, the secondary rhinaria are usually reduced. The hairs on segment III are often measured and used in relation to the width of the basal diameter of the segment (Ilharco and & van Harten, 1987; Millar, 1990; Blackman & Eastop, 2000).

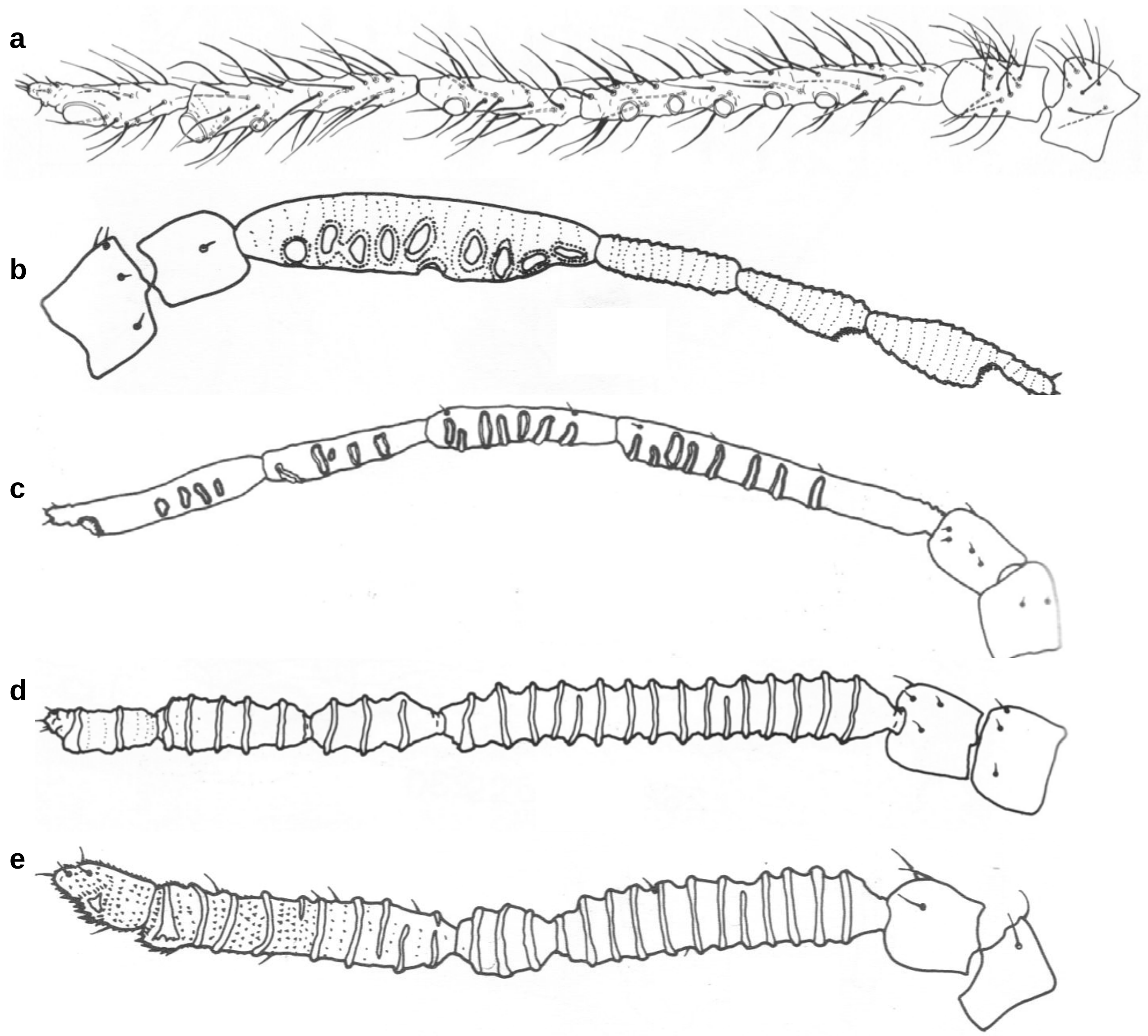

Fig. 2.6. Types of secondary rhinaria. Rounded (a), oval (b), transversely elongate (c), very elongate (d) and ring like (e).

2.3.3 Abdomen and related features

Various body shapes are found within the Aphidoidea, and could be a useful characteristic for preliminary identification in combination with other macroscopic characters such as colour and body length. Aphid colour should be noted in the field as it is lost after aphids die. Some aphid species have their own characteristic colour.

For example, *Aphis nerii* (Boyer de Franscolombe) is bright yellow with black siphunculi, whereas other species may show variation in colour. Examples are *Acyrthosiphon pisum* (Harris) than can be green or pink and *Aphis gossypii* that varies from pale yellow, through dirty yellow-green to dark bluish-green almost black from high to lower temperatures (Blackman & Eastop 2007). Body length (1.5 – 3 mm) is usually measured from the centre of the frons to the tip of the abdomen, excluding the cauda. Aphids less than 2 mm in body length are considered small and aphids with body size of more than 3 mm large.

The head and pro-thorax of alatae are always clearly separated, but are fused in the apterae of some groups such as Greenidinae and some other subfamilies. The abdomen comprises eight distinct segments ending in a cauda and anal plate (Fig. 1.1). A pair of rounded, or reniform spiracles occurs on each of the first seven abdominal segments as well as the meso- and meta-thorax. Sclerotization of the abdominal tergites in the form of large dark patches, intersegmental bars and isolated patches can occur on the abdomen (Fig. 2.7). This characteristic displays a lot of variation within species but can still be used as a functional feature (Ilharco & van Harten, 1987; Millar, 1990).

a b c

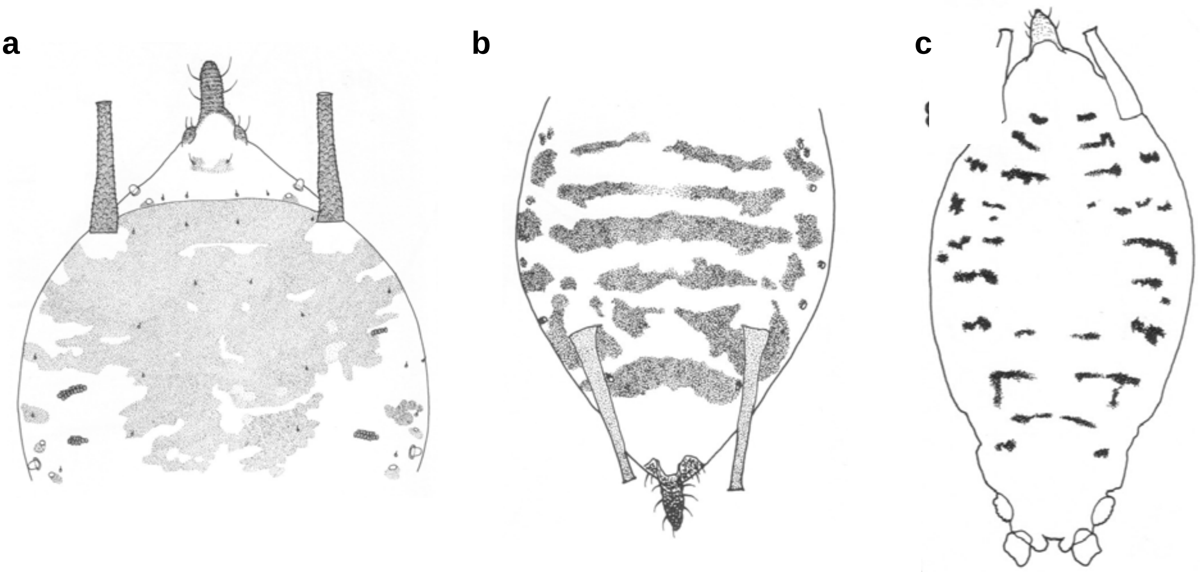

Fig. 2.7. Abdominal sclerotization. Dark patches (a), intersegmental bars (b) and isolated patches (c) (from Millar, 1990).

2.3.4 Abdominal appendages

Aphids have a general form and structure of the legs, with little variation. The main character used in keys is the length and segmentation of the hind tarsi. Generally, aphids have two-segmented tarsi, the second segment mostly elongated, which is compared with the apical rostral segment (Fig. 2.4, 2.5). Some genera of Aphidinae only have one hind tarsal segment, and in some aphids the tarsi are absent (some Hormaphidinae) (Ilharco & van Harten, 1987; Blackman & Eastop, 2000). In some genera the coxae of the first pair of legs are enlarged, perhaps to enable the aphid to extract its mouthparts quicker from the plant and aid escape mechanisms (Millar, 1990).

The siphunculi are situated on the posterior margin of the Vth abdominal segment (Blackman & Eastop, 2000). The siphunculi, a very characteristic feature of the Aphidoidea, are the secretory organs of aphids with their exact function still unexplained (Blackman & Eastop, 2007). Secondary reduction of the siphunculi may occur in some taxa, causing the siphunculi to be absent. Adopting various forms and varying greatly between taxa, they can be reduced to ring-like structures, conical, tapering, clavate, cylindrical, elongate, etc.(Fig. 2.8). The apex can be widened by a distinct flange, the centre of the siphunculi is often swollen causing the siphunculi to be club shaped, and reticulated imbrications may occur on the distal half (Ilharco & van Harten, 1987; Blackman & Eastop, 2000)

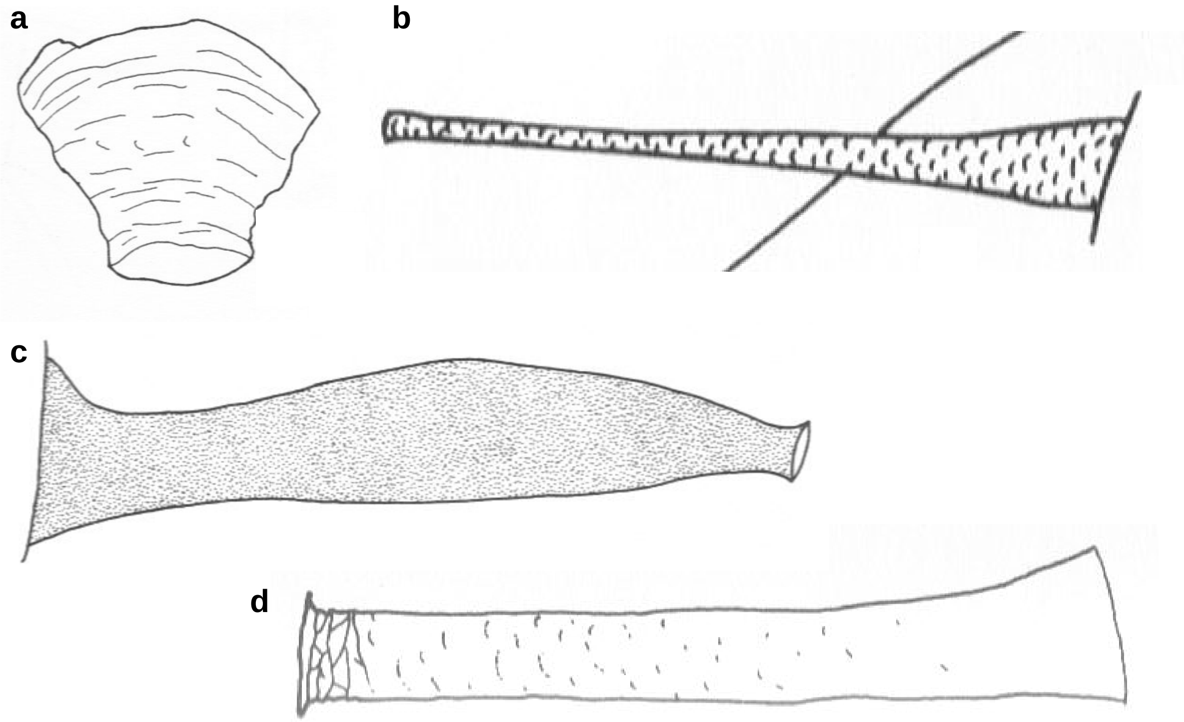

Fig. 2.8. Different shapes of the cauda. Conical (a), tapering (b), clavate (c) and cylindrical (d) (from Millar, 1990).

The shape of the cauda, formed by the sternum of the Xth segment, along with the number of hairs it contains is a valuable taxonomic feature (Millar, 1990). Various shapes are distinguished; rounded, pentagonal or helmet shaped, tongue shaped, triangular, elongate, ensiform, etc. (Fig. 2.9). In Drepanosiphinae and Hormaphidinae the cauda is constricted, separating the basal part from the knob like apex (Ilharco & van Harten, 1987; Millar, 1990; Blackman & Eastop, 2000).

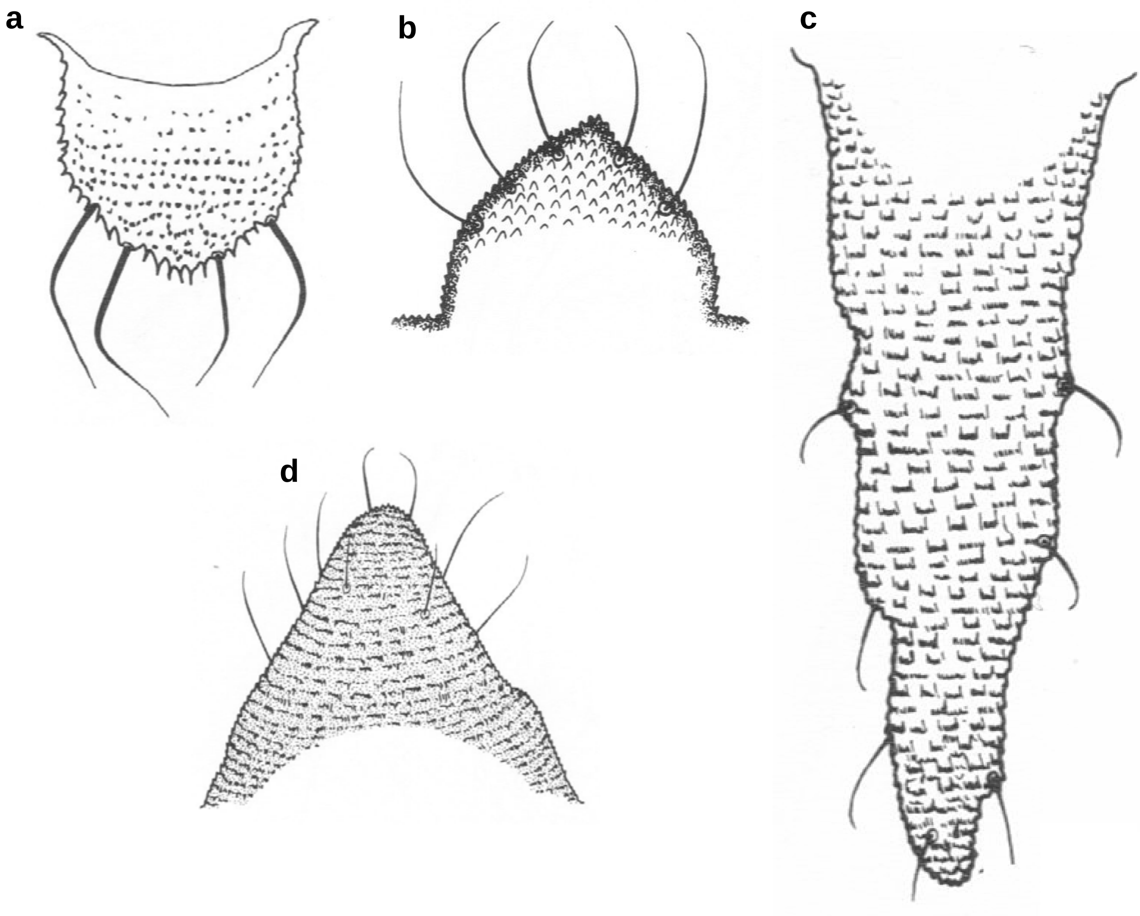

Fig. 2.9. Different shapes of the cauda. Rounded (a), pentagonal (b), triangular (c) and elongate (d) (from Millar, 1990).

Aphids have two pairs of wings, with relatively few veins (Fig. 2.10). The median vein can be simple, once or twice branched, or indistinct. The cubitus (Cu1 and Cu2), are generally separate but may be fused in some Pemphiginae and Hormaphidinae. The oblique vein of the hind wing may be single, double or reduced. In some aphids characteristic pigmentation may be associated with the wing veins apart from the pterostigma (Millar, 1990).

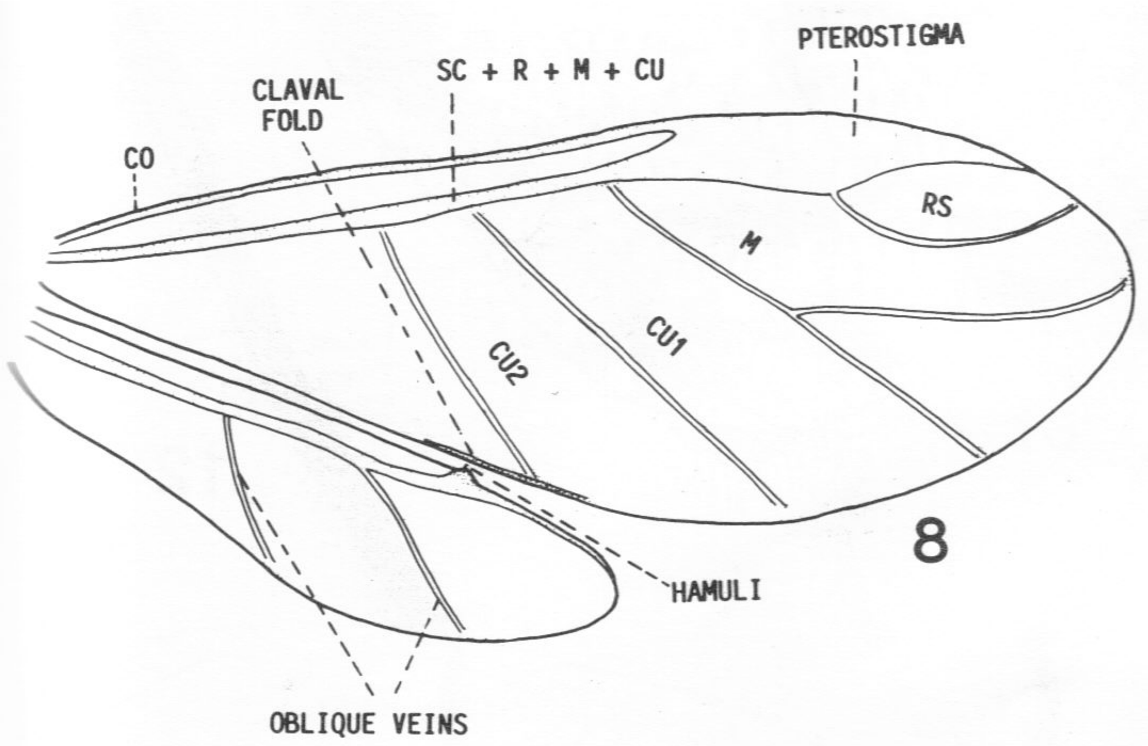

Fig. 2.10. Front and hind wing of alatae (from Millar, 1990).

2.3.5 Tubercles, wax glands and hairs

The term tubercle in Aphidinae refers to small papilla like structures on the abdominal and thoracic margins. In the Aphidini, for example, *Aphis* (L.) and *Rhopalosiphum* (Koch), lateral tubercles are almost always found on the Ist and VIIth abdominal segments. In the Macrosiphini, if such tubercles are present, they are only found on abdominal segments II – V and are pimple-like and strongly projected or small rounded bumps. Protruberances, often referred to as tubercles, are cuticle outgrowths and bear one or two setae. They may be small rounded structures or elongate projections that can be branched, occurring in pairs or as single spinal projections (Millar, 1990).

White waxy particles or filaments are often produced by specialized wax glands. Although not always distinguishable, distinct arrangements occur among taxa. In the Aphidinae they are scattered over certain areas of the cuticle creating a dull or mealy appearance. In the Pemphiginae, groups of wax glands form distinct wax plates. Facets of wax glands arranged along the abdominal margin of some Hermaphidinae produce a waxy fringe (Ilharco & van Harten, 1987; Millar, 1990).

In general, the chaetotaxy of aphids is readily observed in slide mounted specimens. However, the presence of long capitate hairs on the head and proximal antennal segments can be used in specimens preserved in alcohol. For example, the hair on the third antennal segment of *Macrosiphum* (Passerini) is longer than the length of its basal width. They often project from the head and proximal antennal segments. The abdominal hair of some species is too small to observe without slide mounting the specimens. Some species do have long, thick, spine like spatulate, or fan shaped hair, occurring on the abdomen of some taxa, and may be a helpfull taxonomic trait in alcohol preserved specimens. The body may be longitudinally divided into three areas to describe the position of hairs, wax glands and tubercles. A central spinal (mesal) region, a pleural zone on either side of the mesal region, and a marginal area on each side are distinguished (Fig. 2.1) (Ilharco & van Harten, 1987; Millar. 1990; Blackman & Eastop, 2000).

2.4 Aphid life cycles and polymorphism

Two types of life cycles can be distinguished in the Aphidoidea: heteroecious (host alternating) and monoecious (non-host alternating). Each life cycle has its own successive stage that can be characterized by the presence of different morphs, each morphologically adapted to perform a specific function. For example, increased fecundity in apterae morphs reproducing parthenogenetically (Elliot & McDonald, 1976; Dixon, 1977). The different morphs and stages have varying degrees of economic importance depending on the type of host utilized. Spring and summer morphs are commonly found on agricultural crops, where high numbers of apterae cause severe feeding damage and high numbers of alatae are implicated in transmission of potato viruses (Dixon, 1998; Radcliffe & Ragsdale, 2002; Nault *et al*., 2004; Williams & Dixon, 2007).

Aphids migrating between a woody primary and herbaceous secondary host are known to have a heteroecious life cycle. During autumn with a decrease in photoperiod and temperature the aphids start producing alatae gynoparae (prosexual forms) with males which migrate back to the primary host plant (Daiber & Schöll, 1959; Radcliff, 1982). The autumn migration is controlled by an internal biological clock (Dixon, 1977). On the primary host plant the prosexual forms give rise to apterous females through parthenogetic reproduction. Mating occurs followed by oviposition (Daiber & Schöll, 1959; Radcliff, 1982). The fundatrix (parthenogenetic female) hatches in spring and produces the fundatrigenea (parthenogenetic offspring of fundatrix) parthenogenetically. The first two generations occurring in spring have larger gonads that contain more ovarioles than the successive spring generations. This morphological adaptation enables the fundatrigenae to produce large numbers of spring migrants (Wellings, *et al*., 1980; Leather & Dixon, 1981; Dixon & Kundu, 1998).

The alatiform spring migrants migrate to the secondary host plant (Dixon, 1977). Once the alatae migrants have located and established on the secondary host plant they start reproducing parthenogenetically. Secondary hosts usually include herbaceous plants such as various weeds, ornamental plants and many agricultural crops including lucerne, maize, potato, soybean and wheat (Millar & Dürr, 1985; Radcliffe, 1982). On the secondary host plant aphids mainly produce apterous morphs through parthenogenetic reproduction. However, poor nutritional quality of host plants and colony size could provide a stimulus for formation of alatae. As the colony increases or the nutritional quality of the host plant decreases, aphids start to move around on the plant increasing physical contact between them, which is often referred to as the crowding effect. This tactile stimulation is considered to be the most important stimulus in inducing the morph change during crowding in spring and summer (Daiber & Schöll, 1959; Daiber, 1964[a]; Swenson, 1968; Dixon, 1977; Radcliff, 1982; Dixon, 1998; Powell *et al*., 2006). After several generations winged males and gynoparae are produced (Williams & Dixon, 2007). In mild climates, where the winter temperatures do not decrease to the extent of the European winters, aphids may keep on producing parthenogentically throughout the year (anholocyclic) (Daiber & Schöll, 1959).

Aphids remaining on the same host or moving between closely related host plants are known to have a monoecious life cycle. Aphids with a monoeciuos life cycle can have a holocyclic (overwinters in the egg stage) or anholocyclic (overwinters in the parthenogenetic reproducing form) lifecycle (Daiber & Schöll, 1959). Aphids can be either completely anholocyclic or only in certain parts of their distribution where the geographical range of their host pant is smaller than that of their own. The summer and winter host plants of anholocyclic aphids are usually herbaceous being of great economic importance as their host plants usually include agricultural crops (Williams & Dixon, 2007).

In South Africa, alate *Myzus persicae* (Sulzer) were found to migrate from secondary host plants colonized during the winter, i.e. various families of weeds and garden plants, to potato fields just after plant emergence in spring (Daiber, 1962; Daiber, 1964[a]; Daiber, 1965). In contrast, *Macrosiphum euphorbiae* (Thomas) only colonized secondary host plants a few weeks after the potato plants emerged. These secondary host plants were identified as the main aphid and virus source in early spring (Daiber, 1962). As the winter temperatures of South Africa only slightly inhibit plant activity and the propagation of aphids, and plants are abundant in well watered areas of South Africa, mainly anholocyclic overwintering of aphids occurs (Daiber & Schöll, 1959; Daiber, 1964[a]).

2.5 Aphid dispersal and host plant selection behaviour

Spring alate migrants, being the dispersal morph, are able to disperse over great distances and are thus responsible for virus spread into crops (Dixon 1977; Radcliffe & Ragsdale, 2002). Approximately 42 aphid species are known to be able to transmit PVY (Ragsdale *et al*., 2001). However, only 14 species are known to colonize potatoes worldwide (Blackman & Eastop, 2000). Many alatae of aphid species that do not colonize potatoes but are able to transmit PVY have been collected from potato crops in high numbers. Because of the high number of non-colonizing aphid species recorded on potato, it is important to understand how aphids perceive their environment and locate host plants to improve the management of PVY spread.

Alate aphids leaving their original host plant respond to environmental cues, such as light intensity, temperature and wind speed at the surface of the plant, before they initiate flight activity. *Drepanosiphum platanoides* (Schrank) was found to alight frequently in calm winds at temperatures above 13.5 °C. However, flight take-off was inhibited in the evening when light intensity decreased (Haine, 1955). After take-off, aphids enter an obligate migratory phase, during which they fly vertically and disperse with prevailing wind currents. Aphids have been found to fly for periods of up to 8 hours (Cockbain, 1961 ; Loxdale *et al*., 1993). The migratory phase is ended by directed flight. Aphids will then respond to visual and olfactory plant stimuli to locate a possible host plant (Nottingham & Hardie, 1989).

Once aphids have made contact with the surface of a leaf, contact evaluation will commence. During contact evaluation physical features of plants such as epicuticular waxes, trichome exudates, substrate texture, topology and colour may influence the behaviour, although it will not necessarily prevent stylet penetration (Powell *et al*., 2006). Powell *et al*. (1999) found that aphids will attempt to insert their stylets as a tarsal contact reflex. Brief probes of less than 1 minute are made to the epidermis, during which plant sap may be ingested giving the insect early and reliable information about the host plant via a gustatory organ in the epiphyrangeal tract (Powell *et al*., 2006). It is during this initial probing that the aphids acquire and transmit non-persistent plant viruses (Martin *et al*., 1997). Penetration into the mesophyl and parenchyma may follow, which is indicated by probes longer than 30s to a minute, providing further host plant information. Before phloem sieve elements are punctured, watery saliva is injected into sieve elements. This inhibits the sieve elements defensive phloem sealing mechanism and allows phloem penetration and sap excretion. Phloem acceptance may be indicated by feeding periods exceeding 10 minutes and could continue for several hours (Caillaud, 1999; Powell *et al*., 2006). This sequence of behaviours can be ended at any stage, in which case the aphid will take off in search of another possible host plant. Powell & Hardie (2000) showed that spindle, the primary host of *Aphis fabae* (Scopoli), has a taxonomical cue that is located within the epidermal cells and that is detected by *A. fabae* after a short intracellular stylet penetration, inhibiting insect flight.

2.6 Aphid control strategies

2.6.1 Insecticidal control

Chemical control is the dominant approach to aphid control and thus PVY management programmes (Daiber, 1964[b]; Radcliff, 1982). The reasons for this could be the lack of alternative strategies, the difficulty in predicting epidemics before economic losses occur, the methods and application technology of insecticides are familiar and readily available and the cost of chemicals can be relatively low in comparison to total production cost (Perring *et al*., 1999). However, insecticides are generally not effective in reducing aphid-borne non-persistent viruses such as PVY due to the fast acquisition and transmission time (Broadbent, *et al*., 1956; Raccah *et al*., 1980; Collar *et a*l., 1997). For chemical use to be effective in reducing non-persistently aphid transmitted viruses, it has to kill or immobilize the aphid before acquisition and transmission is possible, repel the aphid or modify its behaviour to prevent stylet penetration of the epidermal layer (Perring *et al*., 1999). Synthetic pyrethroids, however, are thought to hold some potential in reducing non-persistent virus spread. Gibson *et al*., (1982), for example, found that the acquisition and transmission of PVY by *M. persicae* was reduced by deltamethrin in greenhouse trials. In accordance with this, Atiri *et al*., (1987) observed that pyrethroid treated plants shortened the probing duration by aphids.

2.6.2 Cultural control

Potato seed growers have been advised to follow good cultural practices in order to reduce virus incidence. Seed potato fields should be isolated from commercial potato fields (Ragsdale *et al*., 2001), because the cultivation of both in the same area will increase virus incidence dramatically, as the potato crop itself is the most common source of inoculum. Different quality seed is used for the production of seed and ware potatoes. For seed potatoes, only certified G0 (virus free) seed should be used, whereas this is not the case for the production of commercial potatoes. Other possible cultural control measures such as removing weeds growing around potato fields could contribute to virus management as they could act as virus inoculum (Radcliffe & Ragsdale, 2002). Roguing fields (removing virus infected plants in the early growing stages of the crop) and removing volunteer potatoes growing out of season and around fields have been proven successful (Thresh, 1988).

2.6.3 Biological control

Biological control of aphids by means of parasitoids (e.g. parasitic wasps) has been successful, for example, for *A. pisum* and *Theoraphis trifolii* (Monell) on alfalfa (Dixon, 1977). However, biological control, including augmentative biological control, of plant virus vectors is rarely feasible. Virus spread occurs with the arrival of viruliferous aphids to the crop (Nault, 1997). Control of the plant virus should thus be targeted at alatae aphids migrating into the crop. Biological control is only effective once the pest has colonized the crop since the population size of the natural enemy is dependent on pest population numbers (Blackman, 1976).

Further, in the case of aphids on commercial crop fields, parasitoid populations are not able to sustain themselves due to the frequent use of insecticides. Aphids are generally considered as a low density pest on potatoes making it much more difficult for the parasitoids to establish a sustainable population (Shands *et al.*, 1972; Radcliff, 1982).

Generalist predators have some potential in controlling aphid populations on the primary host before migrating to the secondary host. The usually polyphagous nature of predators enables populations to sustain themselves on low density pest populations. Coccinellids, syrphids, chrysopids, anthocorids, nabids, and lygaeids are considered as the most important aphid predators. However, spiders have also been reported to reduce aphid populations (Radcliff, 1982; Sunderland, 1999; Symondson *et al*., 2002). In north eastern Main, Shands *et al.*, (1972) found that spiders as a group were probably the most important predators of aphid populations on primary hosts as well as potatoes, the secondary host. Spiders suppressed aphid populations throughout the entire season due to their mobility and seasonal distribution pattern, with highest numbers occurring during and shortly after the aphid's spring migration (Shands *et al.*, 1972).

For biological control to be effective in commercial potato fields it would be beneficial to promote a complex of natural enemies, including generalists and specialists, with a concomitant reduction in insecticide applications (Blackman 1976; Shands *et al.*, 1972).

2.6.4 Crop borders

The use of crop borders has been found to be effective in reducing the spread of non-persistent viruses. Radcliff & Ragsdale (1998), found a reduction in virus spread of 67 %. Similarly, DiFonzo *et al.* (1996) observed significantly lower PVY incidence in crops planted with a border plant. This strategy entails the planting of a different plant around the periphery of a crop. Aphids migrating into the field react on the contrast in colour between the crop and the fallow ground interface at the edge of the field and will land on the border plant before moving into the field proper. By probing the border plant aphids purge their mouthparts, reducing virus transmission when entering the main crop. (Jenkinson, 1955; DiFonzo *et al.*, 1996; Fereres, 2000; Radcliffe & Ragsdale, 2002). The use of crops as border plants is thought to be a relatively easy control measure, if a crop is used that is already part of the crop regime planted in an area, as this does not require any additional specialized equipment and it is compatible with current production practices (Ragsdale *et al*., 2001).

Very few studies have investigated the mechanisms behind crop borders. It has been proposed that the border plant acts as a virus sink, thus reducing the risk of non-persistent virus transmission (Fereres, 2000; Jones, 2005; Hooks and Fereres, 2006). Other factors, such as plant structure, as well as visual and olfactory stimuli contribute to the mechanisms involved in reducing non-persistent virus spread (Hooks & Fereres, 2006). For example, barley planted around clover reduced *Bean yellows mosaic virus* (BYMV) incidence, suggesting that barley acted as a physical barrier, intercepting alatae aphids migrating into the field (Jayasena & Randles, 1985). The border plant may serve as a trap crop, by selecting a plant that is attractive to the virus vector (Nault, *et al*., 2004; Hooks & Fereres, 2006).

The type of crop selected for the border is important, as aphids respond to visual and olfactory cues emitted from their host plants (Powell *et al*., 2006). A plant species susceptible to PVY, such as potato would not be feasible, as it will serve as a virus inoculum. Therefore, it should be best to select a virus non-host as a crop border. Significant reductions of PVY incidence were observed in potato and pepper fields planted with crop border plants not able to host PVY (DiFonzo *et al*., 1996; Fereres, 2000). Damicone *et al*., (2007) found a reduction in the non-persistent *Papaya ring spot virus*-watermelon strain (PRSV-w) in pumpkin planted with a grain sorghum crop border. However, PRSV-w incidence was not reduced when pumpkin was planted with a peanut, soybean or maize border. This supports the suggestion of Nault *et al*., (2004), that a plant species preferred by aphids in comparison to the main crop should be selected as a crop border plant.

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Chapter 3

Evaluating aphid host plant selection to optimize the use of crop borders to reduce incidence of aphid-transmitted *Potato virus Y* (PVY)

Abstract

Crop borders have the potential to reduce the transmission of non-persistent aphid borne viruses if a virus non-host is used as a border plant. Alatae landing in these crop borders purge their mouthparts of the virus by initial probing behaviour on the virus non-host plant before moving into the field proper. The plant species used affects aphid landing, as aphids respond to visual and olfactory cues emitted by their host plants. The aim of the study was to determine aphid host plant preference for selected agricultural crops to identify a potential border plant to reduce *Potato virus Y* (PVY) transmission. Four crops, namely maize, wheat, lucerne, and soybean were evaluated as potential border plants in a semi-field trial. The four crops, together with potato, were planted in a randomized block design. To compare aphid species composition on the different crops aphids were sampled using leaf counts, sweep-netting and green bucket traps to determine landing rates. Three different methods were used to avoid sampling bias caused by a specific method. The three methods gave different results in terms of aphid abundance and showed varying degrees of overlap in species composition among the crops. Overall aphid abundance and species composition suggest maize and wheat as suitable border crops for potato fields for colonizing and non-colonizing species. Landing patterns of alatae indicated that aphids are able to discriminate between plants in the pre-alighting phase. Results

show that more than one sampling method is needed to determine host plant preferences of highly polymorphic insects such as aphids.

3.1 Introduction

Planting a virus non-host plant around a main crop as a crop border has been suggested as an environmentally-friendly way to effectively reduce the spread of non-persistently transmitted viruses by aphids (Jenkinson, 1955; DiFonzo *et al.*, 1996; Radcliffe & Ragsdale, 1998; Fereres, 2000), the rationale being that alatae dispersing into the crop react to the difference in colour between the brown of the fallow ground and the green of the border plant, causing them to alight more frequently on the border (DiFonzo *et al.*, 1996; Ragsdale *et al.*, 2001). Probing the virus non-host plant which acts as a virus sink causes aphids to purge their mouthparts of viral particles before moving into the crop, thus reducing the risk of non-persistent virus transmission (Fereres, 2000; Jones, 2005; Hooks and Fereres, 2006). Other factors, such as plant structure and visual and olfactory stimuli, contribute to aphids' alighting on such border plants (Hooks & Fereres, 2006). For example, barley planted around clover reduced *Bean yellows mosaic virus* (BYMV) incidence, indicating that barley, acting as a physical barrier, intercepted alatae migrating into the clover field (Jayasena & Randles, 1985). Further, a border plant may serve as a trap crop when attractive to the virus vector (Damicone *et al.*, 2007). Therefore, aphid host plant selection behaviour plays an important role in the effective use of crop border plants.

Alatae do not seem to discriminate between host and non-host plants before alighting on a plant (Kennedy *et al.*, 1959; Orlob, 1961). After landing, aphids insert their stylets into the sub-epidermal layer of plants as a tarsal contact reflex, ingesting small amounts of leaf sap (Caillaud, 1999; Powell *et al.*, 2006;). During this initial brief probing of the plant, aphids evaluate the plant sap while acquiring or transmitting non-persistent viruses. Therefore, some consideration should be given to selecting the type of plant to be as a crop border. Plant species susceptible to PVY, such as potato, are not feasible, because they can serve as a virus inoculum. Therefore, a virus non-host should be selected as a crop border plant. Considerable reductions in PVY incidence (up to 13 %) were observed in potato and pepper fields with crop borders consisting of virus non-host plants (DiFonzo *et al*., 1996; Fereres, 2000). Damicone *et al*. (2007) observed a reduction in the non-persistent *Papaya ring spot virus-watermelon strain* (PRSV-w) in pumpkin planted with a grain sorghum crop border. However, PRSV-w incidence was not reduced when pumpkin was planted with a peanut, soybean or maize border. It is possible that that sorghum, being a host plant of the key vector species *(Rhopalosiphum maydis)* recorded, inhibited the aphid's take-off response after initial probing. This supports the findings of Nault *et al*. (2004) that a plant species preferred by aphids over the main crop should be selected as a crop border plant.

The seed potato industry in many potato-growing regions throughout the world is suffering from substantial economic losses due to the rapid spread of PVY, which is transmitted non-persistently by aphid vectors. Insecticides are commonly used to control aphids and subsequently the spread of PVY. However, the efficiency of insecticides in preventing virus spread is questionable. Insecticides do not kill or immobilize aphids before they are able to transmit PVY, and may even act as an irritant, causing the aphids to move and probe more frequently, thus increasing the probability of virus transmission. (Fereres, 2000; Ragsdale *et al*., 2001). Similarly, due to the host plant-searching behaviour of alatae, the non-colonizing species of potato that are vectors of PVY play an important role in transmitting the virus in seed potatoes (Swenson, 1968; Raccah *et al*., 1985; Summers *et al*., 1990). Host plant-specific cues may inhibit the take-off response of aphids. In the absence of host plant specific cues viruliferous aphids will take off in search of another plant, increasing the likelihood of PVY transmission (Caillaud, 1999; Powell & Hardie, 2000; Powell *et al*., 2006).

Several cultural control practices, such as reduction of virus inoculum, removing weeds and volunteer potatoes growing in the fields, and spatial and temporal isolation of seed production fields contribute to reducing aphid spread and have become the primary focus of seed certification programmes (Ragsdale *et al*., 2001). The use of crop borders is an additional cultural control method proposed to reduce PVY incidence in seed potatoes (DiFonzo *et al*., 1996).

The preference of aphids for selected agricultural crops was determined to identify a potential border crop. For the purpose of this study, we define preference as a qualitative, behavioural trait that can be measured experimentally and only has meaning within a specified set of plants (Singer, 2000).

Aphid abundance, alatae landing rates and aphid species composition (aphid species occurring in given habitat) were compared between lucerne, maize, soybean and wheat with potato using different collecting methods to eliminate bias caused by methodology.

3.2 Materials and methods

3.2.1 Experimental design

Five crops, potato (*Solanum tuberosum* L., Solanaceae, 'BP1'), lucerne (*Medicago sativa* L., Fabaceae, 'Standaard'), wheat (*Triticum aestivum* L., Gramineae, 'Kariega'), maize (*Zea maize* L., Gramineae, 'CRN 3505') and soybean (*Glycine max* (L.) Merr., Fabaceae, 'Moekwa') were planted in a randomized block design at the University of Pretoria Experimental Farm (Pretoria, South Africa, 25°43'S 28°17'E) in March 2006. The crops were selected based on previous discussions with seed potato growers. The field was subdivided into six blocks. Within each block the five crops were randomly assigned to each of five 5 x 5 m plots with 1 m fallow ground between plots (Fig 3.1).

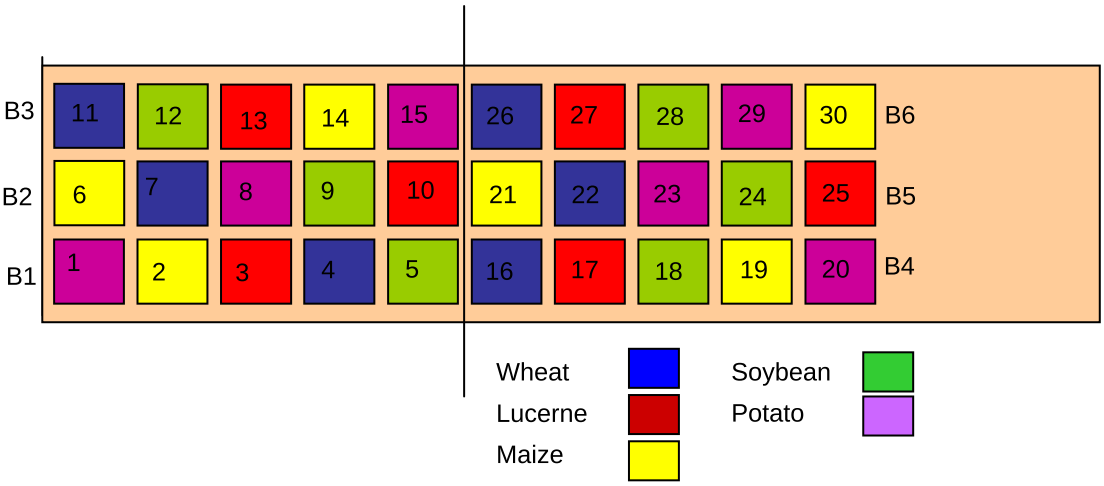

Fig. 3.1. Layout of the crop preference trial at the University of Pretoria Research Farm (randomized block design; B1 – B6: block 1 to block 6; 5 crops/block).

Each plot contained 11 rows of plants. Potato tubers were planted 60 cm apart, and seeds of maize and soybean positioned 20 cm apart. Wheat and lucerne were sown evenly within each row. The distances were selected to ensure an even coverage of the surface area of a plot with plant foliage as far as possible. Crops were fertilized and irrigated according to normal farming practices. No pesticides were applied to the crops during the trial. The crops were naturally infested by aphids.

3.2.2 Aphid sampling and identification

Aphid abundance and species colonizing the crops were determined using three collection methods. Firstly, leaf counts were taken. Ten plants were randomly selected within each plot and the number of aphids found on the four top, middle and bottom leaves was counted. Sub-samples of aphid clusters were collected from each plant for species identification. A new set of 10 random plants, excluding those already sampled, was selected for each sampling week. Plants were randomly selected using the random function in Excel (Microsoft Office XP). Secondly, sweep net samples of aphids were collected using 10 sweeps across two sets of two randomly selected rows of plants. Thirdly, green bucket traps were used to determine aphid landing rates and crop preference in the pre-alighting phase. A single green plastic bucket trap (35 cm x 10 cm), filled with water and with liquid detergent added, was placed in the centre of each plot. The green bucket traps had a hole covered with gauze just below the upper rim to avoid overflowing from rain water. The traps were kept at canopy level of the respective crops throughout the trial.

Aphid counting and collecting commenced six weeks after planting of crops on the 19th of April 2006 and continued in weekly intervals until the 25th of May 2006. The trial had to be terminated after six weeks due to frost setting in. However, green bucket trap catches were collected for seven weeks. Aphids collected by sweep-netting and in green bucket traps were counted and the adult aphids identified to species level with the exception of damaged individuals. *Sitobion* spp. and *Aphis* spp. were identified up to species level where possible. Otherwise all species belonging to these genera were grouped together. Aphid species identifications of sub-samples were verified by I. Millar of the Biosystematics Division of the ARC-Plant Protection Research Institute (ARC-PPRI).

3.2.3 Statistical analysis

Differences in aphid abundance among crops, as well as effects of crop, time and the two effects combined on aphid abundance were determined with Generalised linear model ANOVA with Poisson error structure and log link function using STATISTICA (StatSoft, Inc. 2004, version 7) (McCullagh & Nelder, 1989). The three sampling methods and the similarity of aphid species composition among crops were compared using non-metric multidimensional scaling (MDS) and the Bray-Curtis similarity coefficient (Clarke & Warwick, 2001). Species data were fourth-root transformed to take species with low abundance into account (Clarke & Warwick, 2001). Significant differences in species assemblage between the three different sampling methods were determined using one-way Analysis of Similarity (ANOSIM) based on group averaging and the Bray–Curtis similarity coefficient (Clarke & Warwick, 2001). Significance of the differences in species assemblages among crops could not be determined with ANOSIM because aphid numbers were too low to allow for comparison of groups. Analyses of similarity percentages (SIMPER) were completed to determine the dissimilarity percentages between groups and identify typifying (abundant species typical for a group) and discriminating (species responsible for differences between groups) species. MDS, ANOSIM and SIMPER were performed using PRIMER (Primer 5 version 5.2.9, Clark & Warwick 2001).

3.3 Results

3.3.1 Aphid abundance

The mean number of alatae remained more or less constant over time ranging between 1 and 7 (Fig. 3.2a), whereas the number of apterae counted on leaves of the five crops increased on maize over the six-week sampling period from a mean of 31.17 to 1382.5 (Fig. 3.3a; Table 3.1). Overall, the highest number of aphids was recorded on maize for both apterae and alatae, followed by wheat, potato and lucerne (Table 3.2). Very few leaves with apterae were found on soybean. Due to the high number of zero counts, soybean was excluded from the leaf count method analysis. Alatae and apterae abundance on the different crops, as determined by leaf counts, was the same for all sampling weeks (Table 3.1).

According to the sweep net sampling method the mean number of alatae remained more or less constant during the six-week sampling period, ranging between 1 and 10 with the exception of lucerne in week 20 (Fig. 3.2b). Likewise, the number of apterae remained relatively constant on the different crops, except for lucerne (Fig. 3.2b). In contrast to the leaf counts the highest number of aphids were collected from lucerne using the sweep net method, followed by wheat, potato and maize; hardly any aphids were collected from soybean (Figs 3.3b; Table 3.1). Abundance of alatae and apterae on different crops was independent of sampling time (weeks) (Table 3.1).

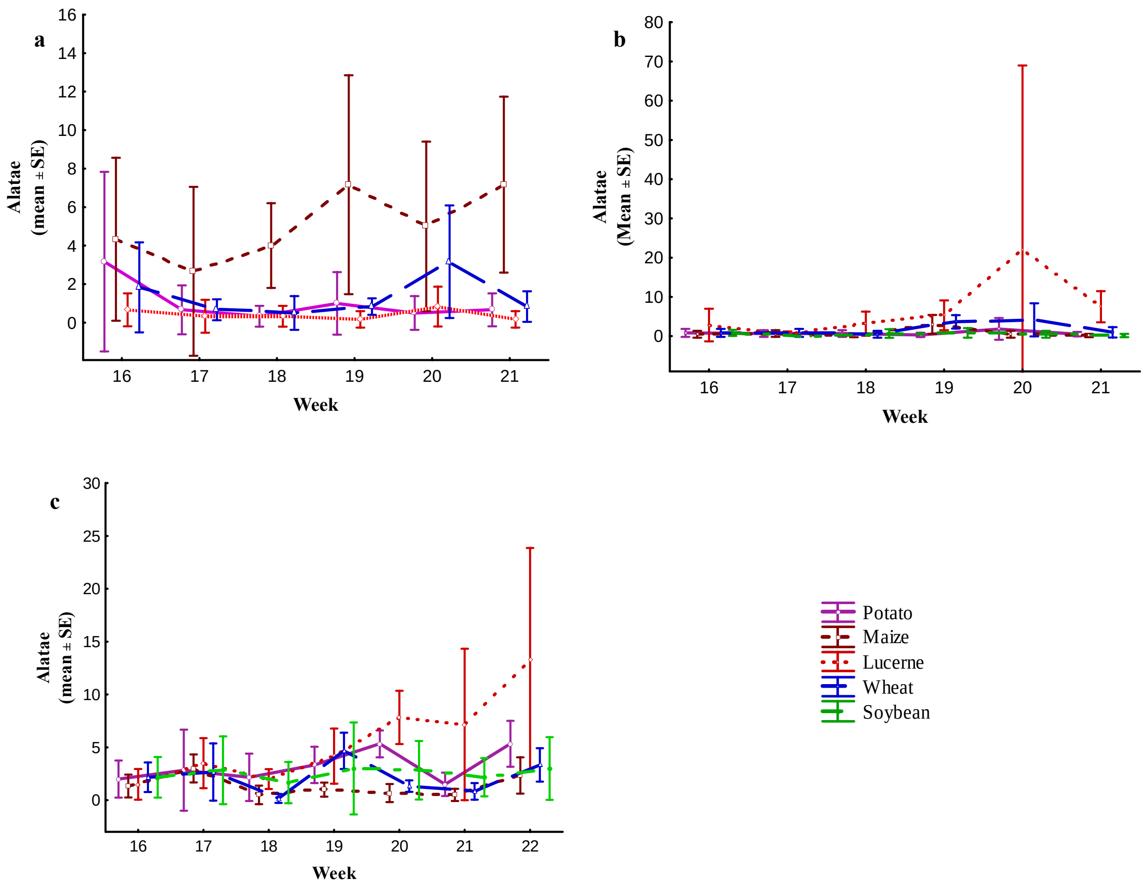

Fig. 3.2. Alatae recorded on lucerne, maize, potato and wheat with leaf counts (a) and sweep net samples (b) and green bucket trap samples (c) on lucerne, maize, potato, wheat and soybean.

Table 3.1. Statistical values for differences in aphid abundance as determined by Generalized Linear Models factorial ANOVA.

	Leaf count			Sweep net			Green bucket		
Effect	**X^2**	**do**	***P***	**X^2**	**df**	***P***	**X^2**	**df**	***P***
Alatae	**Deviance: 44.84**			**Deviance: 47.49**			**Deviance: 42.68**		
Week	8.72	5	0.12	7.58	5	0.18	44.96	6	0
Crop	94.69	3	0	19.72	4	0	50.32	4	0
Week*Crop	21.77	15	0.11	20.38	20	0.43	54.13	24	0
Apterae	**Deviance: 78.9**								
Week	13.39	5	0.01	2.21	5	0.82			
Crop	114.55	3	0	403.08	4	0			
Week*Crop	4.67	15	0.99	10.39	20	0.96			

Overall, aphid landing rates increased over the seven-week sampling period. Similar to the sweep net data, the highest number of aphids alighted on lucerne, followed by potato, wheat, soybean and maize (Fig. 3.2c). In contrast to the leaf count and sweep net data, aphid landing rates over the trial period were not the same for all crops (Table 3.1). An increase in aphid landing rate was observed on lucerne from week 19 to week 22, whereas the number of aphids alighting on the other crops stayed more or less constant (Fig. 3.2c).

Of the 8,436 aphids collected, 3,245 were adults, 4,972 nymphs and 219 damaged individuals. Adults were identified to species level. Appendix B contains a list of the 36 aphid species recorded during the trial. The sub-samples collected from leaves comprised 1,183 individuals and 19 species, those from the sweep net samples 1,567 individuals and 21 species, and those from the green bucket trap samples 495 individuals and 31 species. Overall, the most abundant species were *Acyrthosiphon kondoi* (Shinji), *Macrosiphum euphorbiae* (Thomas), *Acyrthosiphon pisum* (Harris), *Metapolophium dirhodum* (Walker), *Tetraneura fusiformis* (Sasaki), and *Rhopalosiphum padi* (L.).

Table 3.2. Mean aphid abundance on potato, maize, lucerne, wheat and soybean determined by leaf count, sweep net and green bucket trap sampling methods.

Crop	Leaf count Mean ± SE	Sweep net Mean ± SE	Green bucket Mean ± SE
Alatae			
Lucerne	0.42 ± 0.12	6.94 ± 3.09	5.64 ± 0.92
Maize	5.06 ± 0.7	0.83 ± 0.24	1.33 ± 0.2
Potato	1.06 ± 0.36	0.81 ± 0.21	3.21 ± 0.37
Soybean	0.45 ± 0.17	0.50 ± 0.14	2.52 ± 0.39
Wheat	1.31 ± 0.29	1.83 ± 0.39	2.17 ± 0.3
Apterae			
Lucerne	8.83 ± 1.94	123.00 ± 17.69	
Maize	530.69 ± 111.28	2.03 ± 0.89	
Potato	15.86 ± 2.61	2.33 ± 0.56	
Soybean	3.56 ± 1.43	0.61 ± 0.16	
Wheat	56.42 ± 9.77	6.22 ± 1.27	

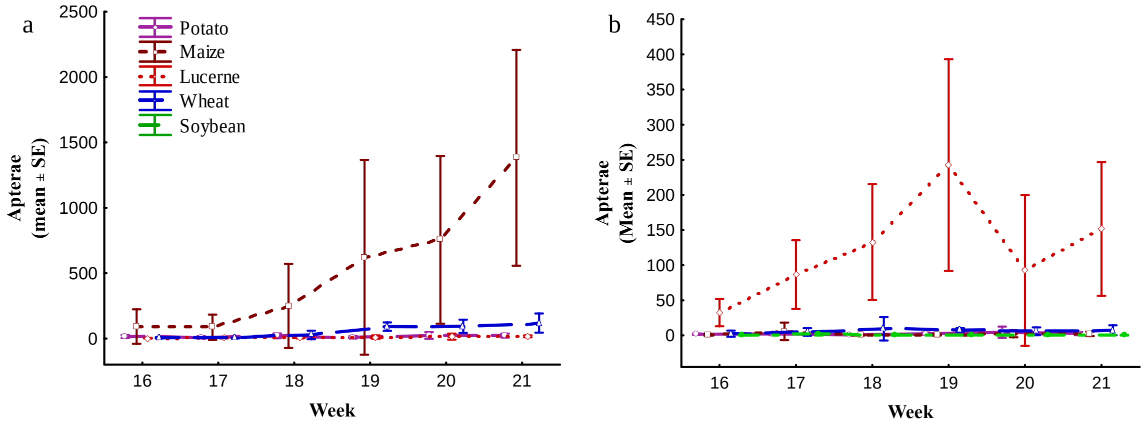

Fig. 3.3. Abundance of apterae counted on four top, middle and bottom leaves from lucerne, maize, potato and wheat (a) and collected with sweep net samples from lucerne, maize, potato, soybean and wheat (b) over a period of six consecutive sampling weeks.

3.3.2 Sampling methods

Species composition and abundance differed according to the method used. The leaf count method gave different results than the sweep net and green bucket trap methods (Fig. 3.4). These findings were confirmed with the one-way ANOSIM (Global $R = 0.378$; $P < 0.001$). The leaf count method differed significantly from the green bucket ($R = 0.512$; $P < 0.001$) and sweep net method ($R = 0.512$; $P < 0.001$), and the sweep net method from the green bucket ($R = 0.272$; $P < 0.001$).

3.3.3 Crop effects within methods

Aphid species colonizing the crops based on leaf counts differed among the crops, with some overlap between maize and wheat (Fig. 3.5a). Different patterns were observed for the sweep net and green bucket trap methods. The MDS configuration for the sweep net samples indicated an overlap in species assemblages between maize, potato and wheat (Fig. 3.5b). Lucerne samples form a distinct cluster and had the highest and soybean the lowest within-group similarity and between-group dissimilarity in comparison to the other four crops (Fig. 3.5b; Tables 3.3, 3.4). Two species, *Acyrthosiphon kondoi* and *A. pisum*, were identified to be typifying of lucerne only, contributing over 70% to the within-group similarity (Table 3.3). Maize and wheat were found to have the most similar species assemblages, followed by maize and potato. *Rhopalosiphum padi* was typifying for maize and wheat, and *Macrosiphum euphorbiae* for maize and potato for the leaf count method. *Tetraneura fusiformis* was typifying on both maize and potato for the sweep net method (Table 3.3).

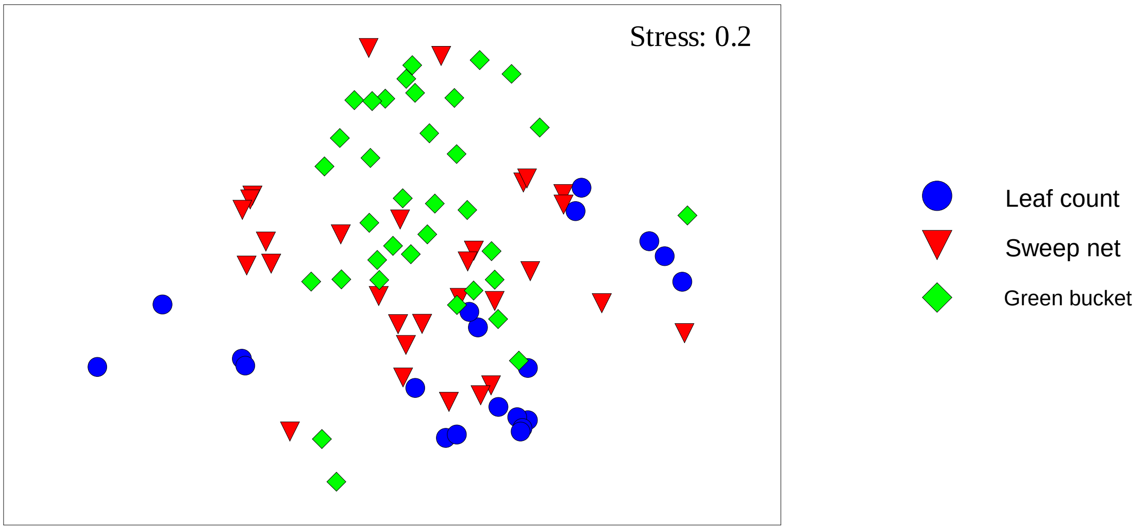

Fig. 3.4. Multidimensional scaling (MDS) ordination showing aphid species assemblages sampled using three different sampling methods.

Compared to the leaf count and sweep net method the MDS plot for the green bucket trap samples indicates more variation and less distinct separation based on species composition between crops (Fig. 3.5c). Lucerne and potato were found to be most similar, followed by potato and wheat, all with *Tetraneura fusiformis* as typifying species. However, similar to the leaf count and sweep net method, *A. pisum* was found to be typifying of lucerne only and *R. padi* of maize (Table 3.3).

The species identified as the most typifying or abundant aphids for the different crops (Table 3.3) accounted for a substantial amount of the dissimilarity in species composition and abundance between the crops. With regard to discriminating species, more species were responsible for the dissimilarity in species assemblage between crops for the green bucket method than the leaf count and sweep net method (Tables 3.4, 3.5).

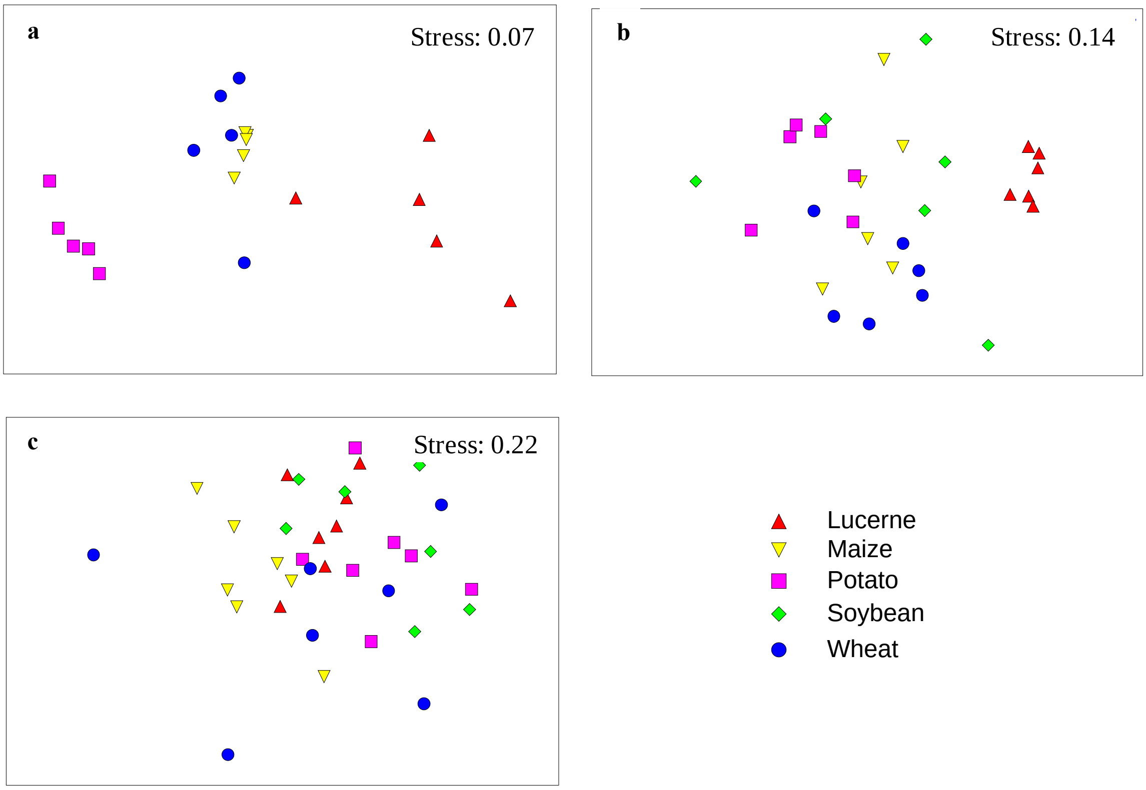

Fig. 3.5. Multi-dimensional scaling (MDS) ordination showing differences in aphid samples identified from leaf count sub-samples collected from lucerne, maize, potato and wheat (a), sweep net samples (b) and green bucket trap samples (c) collected from lucerne, maize, potato, soybean and wheat.

However, similar species were responsible for all or a part of the differences between the crops for all three methods. *Acyrthosiphon kondoi* and *A. pisum* were mainly responsible for the difference in between-group variation with regard to aphid species assemblage between lucerne and the other crops. *Metapolophium dirhodum* and *R. padi* were collected from both maize and wheat and identified as discriminating species between these crops for all three methods. Both species were more abundant on maize using the leaf count and green bucket method, but more abundant on wheat for the sweep net method. In the green bucket trap catches, *T. fusiformis* contributed to most of the dissimilarity between all the crops except for potato and lucerne. Very few *T. fusiformis* individuals were recorded from the leaf count samples and only some from the sweep net samples (Tables 3.4, 3.5).

Table 3.3. Similarity between crops and percent contribution of typifying species at the 50 % cut-off point. Asterisks indicate known vectors of PVY. C indicates species colonizing potatoes.

Method	Crop	Aphid species	% Contribution
Leaf count	**Lucerne**	*Acyrthosiphon kondoi*	43.87
	(Average similarity: 46.82 %)	*Acyrthosiphon pisum* *	41.5
	Maize	*Macrosiphum euphorbiae* *,C	32.65
	(Average similarity: 78.88 %)	*Rhopalosiphum padi* *	27.29
	Potato	*Macrosiphum euphorbiae* *,C	54.3
	(Average similarity: 64.79 %)		
	Wheat	*Metapolopium dirhodum* *	38.08
	(Average similarity: 60.43 %)	*Rhopalosiphum padi* *	32.26
Sweep net	**Lucerne**	*Acyrthosiphon kondoi*	40.02
	(Average similarity: 76.91 %)	*Acyrthosiphon pisum* *	34.46
	Maize	*Rhopalosiphum padi* *	37.23
	(Average similarity: 45.96 %)	*Tetraneura fusiformis*	44.48
	Potato	*Macrosiphum euphorbiae* *,C	45.72
	(Average similarity: 57.86 %)	*Tetraneura fusiformis*	26.02
	Wheat	*Metapolophium dirhodum* *	26.94
	(Average similarity: 52.22 %)	*Rhopalosiphum padi* *	35.72
Green bucket	**Lucerne**	*Acyrthosiphon pisum* *	16.46
	(Average similarity: 46.33 %)	*Tetraneura fusiformis*	46.54
	Maize	*Macrosiphum euphorbiae* *,C	19.88
	(Average similarity: 48.41 %)	*Rhopalosiphum padi* *	33.41
	Potato	*Tetraneura fusiformis*	92.05
	(Average similarity: 45.15 %)		
	Wheat	*Tetraneura fusiformis*	55.82
	(Average similarity: 25.38 %)		

Table 3.4. Dissimilarity between crops and percentage contribution of discriminating species at the 50 % cut-off point as determined by the leaf count and sweep net method. Asterisks indicate known vectors of PVY. C indicates species colonizing potatoes.

Method	Crops	Aphid species	% Contribution
Leaf count	**Lucerne vs. Maize**	*Macrosiphum euphorbiae* *,C	23.65
	(Average dissimilarity: 81.28 %)	*Metapolophium dirhodum* *	14.49
		Rhopalosiphum padi *	18.51
	Lucerne vs. Potato	*Acyrthosiphon kondoi*	15.43
	(Average dissimilarity: 94.49 %)	*Macrosiphum euphorbiae* *,C	20.69
		Myzus persicae *,C	16.83
	Lucerne vs. Wheat	*Acyrthosiphon kondoi*	14.74
	(Average dissimilarity: 81.36 %)	*Acyrthosiphon pisum* *	13.19
		Metapolophium dirhodum *	14.56
		Rhopalosiphum padi *	14.99
	Maize vs. Potato	*Metapolophium dirhodum* *,C	21.64
	(Average dissimilarity: 74.23 %)	*Myzus persicae* *,C	11.92
		Rhopalosiphum padi *	21.79
	Maize vs. Wheat	*Macrosiphum euphorbiae* *,C	34.42
	(Average dissimilarity: 41.05 %)	*Metapolophium dirhodum* *	12.28
		Rhopalosiphum padi *	14.83
	Potato vs. Wheat	*Macrosiphum euphorbiae* *,C	13.00
	(Average dissimilarity: 82.38 %)	*Metapolophium dirhodum* *	20.21
		Myzus persicae *,C	12.44
		Rhopalosiphum padi *	15.10
Sweep net	**Lucerne vs. Maize**	*Acyrthosiphon kondoi*	29.92
	(Average dissimilarity: 79.8 %)	*Acyrthosiphon pisum* *	26.38
	Lucerne vs. Potato	*Acyrthosiphon kondoi*	26.83
	(Average dissimilarity: 80.19 %)	*Acyrthosiphon pisum* *	23.83
	Lucerne vs. Wheat	*Acyrthosiphon kondoi*	21.63
	(Average dissimilarity: 78.13 %)	*Acyrthosiphon pisum* *	18.60
		Metapolophium dirhodum *,C	9.59
		Rhopalosiphum padi *	9.04
	Maize vs. Potato	*Aphis* spp. *	12.39
	(Average dissimilarity: 60.1 %)	*Macrosiphum euphorbiae* *,C	19.34
		Myzus persicae *,C	13.53
		Rhopalosiphum padi *	15.91
	Maize vs. Wheat	*Metapolophium dirhodum* *	17.13
	(Average dissimilarity: 57.52 %)	*Rhopalosiphum padi* *	9.90
		Sitobion spp.	16.43
		Tetraneura fusiformis	10.62
	Potato vs. Wheat	*Macrosiphum euphorbiae* *,C	8.98
	(Average dissimilarity: 67.92 %)	*Metapolophium dirhodum* *	14.17
		Rhopalosiphum padi *	14.09
		Sitobion spp.	13.31

Table 3.5. Dissimilarity between crops and percentage contribution of discriminating species at the 50 % cut-off point as determined by the green bucket trap method. Asterisks indicates known vectors of PVY. C indicates species colonizing potatoes.

Method	Crops	Aphid species	% Contribution
Green bucket	**Lucerne vs. Maize**	*Acyrthosiphon kondoi*	9.93
	(Average dissimilarity: 65.52 %)	*Acyrthosiphon pisum* *	12.15
		Macrosiphum euphorbiae * c	9.44
		Metapolophium dirhodum *	9.48
		Tetraneura fusiformis	12.33
	Lucerne vs. Potato	*Acyrthosiphon kondoi*	11.20
	(Average dissimilarity: 59.84 %)	*Acyrthosiphon pisum* *	13.84
		Macrosiphum euphorbiae * c	7.16
		Myzus persicae * c	6.72
		Rhopalosiphum padi *	8.73
		Sitobion spp.	7.11
	Lucerne vs. Wheat	*Acyrthosiphon kondoi*	9.95
	(Average dissimilarity: 66.61 %)	*Acyrthosiphon pisum* *	11.56
		Macrosiphum euphorbiae * c	6.03
		Rhopalosiphum padi *	7.81
		Sitobion spp.	6.90
		Tetraneura fusiformis	10.14
	Maize vs. Potato	*Macrosiphum euphorbiae* * c	12.79
	(Average dissimilarity: 70.25 %)	*Metapolophium dirhodum* *	12.19
		Rhopalosiphum padi *	12.93
		Tetraneura fusiformis	18.20
	Maize vs. Wheat	*Macrosiphum euphorbiae* * c	13.31
	(Average dissimilarity: 69.18 %)	*Metapolophium dirhodum* *	11.89
		Rhopalosiphum padi *	10.73
		Sitobion spp.	8.53
		Tetraneura fusiformis	13.35
	Potato vs. Wheat	*Brachycaudus* spp.	3.95
	(Average dissimilarity: 66.39 %)	*Macrosiphum euphorbiae* * c	5.39
		Myzus persicae *	4.64
		Rhopalosiphum padi *	10.59
		Sitobion spp.	9.67
		Tetraneura fusiformis	16.46

3.4 Discussion

This study confirms that aphid sampling methods can influence results. Sampling of immigrating insects should be treated differently to that of foliar insects as dispersal of immigrant insects can distort data (Kuno, 1991). With regard to alatae migrating into the different crops, cylindrical traps (sticky traps and suction traps) were found to give a better estimate of the aphid species and abundance per unit of volume air, whereas horizontal traps (water bucket traps and flat sticky traps) performed better at estimating aphid species composition and abundance of alatae in the landing phase (Heathcote, 1957; Brook, 1973). Many aphid species are yellow-sensitive and the use of yellow bucket traps will overestimate landing rates. Therefore, green bucket or tile traps are commonly used to determine aphid landing rates (Hodgson & Elbakhiet, 1985; Raccah *et al.*, 1985; Webb *et al.*, 1994; Basky, 2002; Döring *et al.*, 2004; Nault *et al.*, 2004). The green is thought to resemble the colouring of leaves and therefore does not attract aphids as strongly as yellow. It gives a reflection of landing rates and samples all aphid species, including virus vectors, that may land in crops. However, green bucket traps have been shown to sample colonizing species at a lower rate than is reflected by direct counts (Raccah *et al.*, 1985). Therefore, additional methods should be used to determine aphid host plant preference in the pre- and post-alighting phases. Morris (1960) suggests that the use of small stratified sampling units, such as direct counting of insects from leaves, is optimal to sample foliar insects. Therefore the difference in results obtained from the leaf count and green bucket trap method in the present study is expected, and should be used in combination to determine aphid host plant preference in the pre- and post-alighting phase.

Other factors involved in influencing aphid sampling are aphid polymorphism and plant canopy structure (Dixon, 1977; Topping & Sunderland, 1992). The three different methods used in the plant study gave different results not only for species composition but also abundance. The green bucket trap method indicated that aphid abundance remained more or less constant, whereas the leaf count and sweep net methods showed an increase in aphid abundance over time. These contradicting results are due to the green bucket method sampling only alatae and the leaf count and sweep net method sampling both apterae and alatae. After settling on and colonizing of a host plant, apterae will not readily move from the host plant as they invest the majority of their resources in reproduction. It is the alatae that invest most of their resources in distribution and locating host plants to start new colonies (Dixon, 1977; Dixon, 1985; Müller *et al*., 2001).

The difference in plant canopy structure between lucerne and maize could be responsible for the difference in aphid abundance between the leaf count and sweep net sampling methods. The leaf count method underestimated aphid abundance on lucerne most likely due to the small leaf area of lucerne plants. Compared to maize, however, the sweep net sampling method underestimated aphid abundance on maize. It was only possible to sweep the top leaves of the maize plants without damaging the plants and most of the aphids were found on the bottom leaves. Within-plant distribution of apterous aphids varies with aphid species and season. For example, *Aulacorthum solani* (Kaltenbach) preferred to feed on the top and bottom leaves of potato plants (Down *et al*., 1996). *Brevicoryne brassicae* (L.) changes feeding site preference as the season progressed from the top and middle leaves to the middle and bottom leaves (Church & Strickland, 1954). Therefore, leaf counts and sweep netting should be used in combination to sample apterae aphids when comparing aphid species assemblage and abundance between plants with different canopy structures.

With regard to aphid landing, alatae showed the ability to discriminate between host plants in the pre-alighting phase, landing more frequently on the crops they colonized in the current study. *Acyrthosiphon pisum* showed a preference for lucerne and *R. padi* for maize in all three sampling methods. This suggests that aphids have the ability to locate their preferred host plant within a habitat patch. This is contradicting previous studies, which showed that aphids only discriminate between host and non-host plants after landing on the plant and then accepting or rejecting the plant based on surface and sub-epidermal characteristics (Dixon, 1985; Powell & Hardie, 2000; Margaritopoulos *et al*., 2005; Powell *et al*., 2006). On the other hand, olfactory cues from host plants may have an effect on aphids at a distance from the plant by attracting or repelling them (Nottingham *et al*., 1991). Nottingham & Hardie (1993) found that volatiles of summer savoury (*Satureja hortensis* L.) and tansy (*Tanacetum vulgare* L.) deterred *A. fabae* in the pre-alighting phase.

In general, all aphids respond positively to yellow traps (Heathcote, 1957). The apparent attraction to saturated yellow is, however, subject to light intensity and varies between species. Slight differences in the spectral reflectance between leaves of different plants may influence the landing response of alatae (Döring & Chittka, 2007). The findings of the current study raise questions on how aphids relate to host plant-specific cues during the pre-alighting phase of host plant selection behaviour. Therefore further laboratory testing will be needed to determine and compare the attractiveness of the specific host plant cues between potato and the other crops to obtain a better understanding of the mechanism involved in aphid host plant selection.

Due to the commonly observed non-specific landing behaviour of most aphid species, non-colonizing aphids alight in potato fields in high numbers, an important factor to consider when evaluating different plants for a potential crop border plant. After alatae land on plants, they will insert their mouthparts into the epidermal layer of the plant and ingest small amounts of leaf sap as a tarsal contact reflex (Powell *et al*., 1999). During this initial probing behaviour aphids evaluate the plant sap while transmitting PVY before either continuing with probing or rejecting the host plant (Fereres, 2000; Powell *et al*., 2006). Non-colonizing aphid species can contribute to a high primary infection rate in crop fields when occurring in high numbers. This is especially a problem at the end of the season during aphid migration or when other fields in the area are burned off or harvested (Swenson, 1968; Raccah *et al*., 1985; Fereres *et al*., 1993).

In the present study, only two of the recorded aphid species, *M. euphorbiae* and *M. persicae* (Thomas), were known potato colonizers (Millar, 1994). Both species are able to transmit PVY. *Myzus persicae*, however, had very low abundance on potato as well as on the other crops, whereas *M. euphorbiae* was more abundant on maize than potato (Appendix B). All the other aphid species do not colonize potatoes and are able to transmit PVY, except *A. kondoi*, *Sitobion* spp. and *T. fusiformis*, where it is not known if they are vectors. The two most abundant non-colonizing species were *T. fusiformis* and *R. padi*. It is not known if *T. fusiformis* colonized any of the crops during the trial as it is a root feeding aphid. *R. padi*, was typifying for maize and wheat indicating the preference of this species for these two crops over potato.

In conclusion, the sweep net sampling method shows lucerne to be preferred in terms of aphid abundance. These high numbers were mainly due to *A. pisum,* a vector of PVY, and *A. kondoi*. Maize and wheat had the most similar species composition and more species in common with potato than lucerne, as determined by the leaf count and sweep net method. Aphid landing rates, however, indicate lucerne to be most similar to potato in terms of species composition. This is due to the high number of *T. fusiformis* that alighted on both potato and lucerne. Due to the high variation in results between the sampling methods more than one sampling method should be used to determine aphid host plant preference between selected crops for the use of barrier crops. Based on the combined results of the three different methods, maize and wheat were identified as the two most preferred crops to potato in comparison with lucerne and soybean.

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Chapter 4

Comparison of aphid species assemblages between a heterogeneous and a homogeneous agro-ecosystem

Abstract

The intensification of agricultural practices has led to a decrease in species diversity and an increase in pest population outbreaks in agro-ecosystems. Agro-ecosystem stability could be restored by diversification of agricultural landscapes. Crop border plants could possibly contribute to within-field diversification. The aim of this study is to compare aphid species assemblages between (a) heterogeneous and homogeneous plantings and (b) two regions, to evaluate the possibility of implementing management decisions based on a study conducted in one region (Pretoria, Gauteng, RSA) in an agro-ecosystem of another region (Christiana, western Free-State, RSA). Aphid species diversity was higher in the homogeneous plantings of Christiana. Differences in aphid species assemblage between the heterogeneous and homogenous plantings and the two regions are attributed to sampling effects and differences in the surrounding landscape structure. It is concluded that management decision-based on a study conducted in one region may be applicable in an agro-ecosystem of another region.

4.1 Introduction

Landscape heterogeneity (floristic diversity) is positively correlated with species diversity (Benton *et al*., 2003; Weibull *et al*., 2003). Many studies have shown homogenous agricultural landscapes (characterized by the production of one crop species) support a lower species diversity for a variety of taxa, such as small mammals, birds, arthropod predators & insects (Donald *et al*., 2000; Sunderland & Samu, 2000; Schneider & Fry, 2001; Benton *et al*., 2003; Hole *et al*., 2005; Rundlöf & Smith, 2006). The intensification of agricultural practices made this more evident (Krebs *et al*., 1999; Benton *et al*., 2003). The instability of agro-ecosystems, caused by the transformation of heterogeneous landscapes into crop monocultures is characterized by an increase of insect pests on crops (Altieri & Letourneau, 1982). With the prevailing planting of monocultures, primary production is negatively affected by growing pest populations, leading to further intensification of agricultural practices (Altieri, 1999). Due to a reduction in plant diversity and the intensive use of agro-chemicals species richness and abundance of natural enemies have decreased in arable land, rendering management of insect pest populations more difficult (Brust *et al*., 1986; Haughton *et al*., 1999; Sunderland & Samu, 2000).

Increasing landscape heterogeneity could lead to a reduction in pest population abundance and density by increasing species diversity of arthropods. This can be achieved on different spatial scales and the following studies are examples of how landscape heterogeneity can influence species richness of arthropods. Jonsen & Fahrig (1997) found a positive relationship between species richness and abundance of insect generalists feeding on lucerne and the number of habitat patch types in the landscape. They argue that generalist insect species would be able to persevere in homogenous fields (acting as a sink) providing that crop fields are supplemented from species inhabiting and dispersing from surrounding vegetation patches (acting as a source) on a population level. Further, on a landscape scale, Holland & Fahrig (2000) found that woody borders increased herbivorous insect diversity within agro-ecosystems, supporting the suggestion that non crop habitat has a source/sink relationship with crop fields. In a mosaic landscape, non-cropped habitat connecting crop fields increase the heterogeneity of the farming landscape, thus providing increased refuges, feeding areas and movement corridors, promoting species richness (Östman *et al.*, 2001; Benton *et al.*, 2003). In addition, within-field heterogeneity (structure and complexity of the vegetation) has been highlighted as an important factor in agro-ecosystems (Benton *et al.*, 2003). Harwood *et al.* (2001) found that lyniphiid spider web locations were positively correlated with patches of high density prey in winter wheat fields. It is unknown if the web locations were a direct result of prey aggregation or a secondary outcome of vegetation structure and microhabitat factors such as humidity. Agricultural ecologists, therefore, argue that agro-ecosystem stability, i.e. reduced intensity of pest populations and increased abundance and diversity of natural enemies, can be restored by increasing biodiversity in monocultural landscapes (Altieri & Letourneau, 1982; Altieri, 1999). Agricultural diversification can be achieved through intercropping, undersowing, mulches, reducing tillage and utilizing field margins (Dennis & Fry, 1992; Koricheva *et al.*, 2000; Sunderland & Samu, 2000; Hooks & Johnson, 2004; Cai *et al.*, 2007). This would suggest that the use of crop borders (planting a different plant species around the periphery of a crop field) could improve agricultural diversification on the within-field scale. Agricultural diversification increases plant species diversity and structural complexity, providing a variety of food resources, feeding areas, refuges and movement corridors (Östman *et al.*, 2001; Benton *et al.*, 2003). Diversification of productive biota (crops, trees & animals in the system) increases the abundance and species richness of arthropod predators, parasitoids, pollinators and microbial organisms involved in decomposition. This in turn decreases density (number of species per area or unit measured) and abundance of insect pest organisms as well as other pathogens causing damage to crops (Altieri, 1999).

In the present study, the landing patterns of alatae (Hemiptera: Aphididae) in potato fields were investigated. Aphids are important agricultural pests causing yield reductions directly by extracting large amounts of phloem sap from the plants, and indirectly, by transmitting plant viruses, such as *Potato virus Y* (PVY). PVY is a non-persistantly transmitted virus causing degradation of the seed stock, leading to yield losses of 10-100% (Radcliffe, 1982). Aphid species with high transmission efficiency, such as *Myzus persicae* (Sulzer), are considered most dangerous with regard to spreading diseases. However, high numbers of aphid species with low transmission efficiency, e.g. *Rhopalosiphum padi* (L.) could be just as threatening to a seed potato farmer (Radcliffe, 1982; Ragsdale *et al*., 2001). A possible control strategy for the spread of PVY is the use of crop borders. Aphids react to the contrast in colour between the crop and the fallow ground interface at the edge of a field. It has been suggested that a different crop planted around the edge of a potato field, could decrease PVY incidence, provided that the crop is not a host of PVY. Aphids migrating into the potato field, responding to the “edge effect”, would land in the border crop first. Due to the non-persistent manner of PVY, these aphids would lose their ability to transmit the virus after initial probing of the crop border plant (DiFonzo *et al*., 1996; Fereres, 2000; Radcliffe & Ragsdale, 2002). Planting a crop border changes the structural complexity of the crop and increases diversification. Several mechanisms have been proposed to be involved. The crop border could act as a virus sink when selecting a non-host, a physical barrier blocking aphids’ migrating into a field or act as a trap crop when a preferred host plant is used for the border crop. In addition, it can camouflage or mask the main crop by decreasing the ratio of plant-to-soil background. (Hooks & Fereres, 2006).

The aim of this study was to compare aphid species assemblages between (a) heterogeneous and homogeneous plantings, and between (b) two regions, Pretoria (Gauteng, South Africa) and Christiana (western Free State, South Africa). Specific objectives were to determine (i) whether there is a difference in aphid species richness between a homogeneous and heterogeneous crop field, (ii) to determine differences in aphid species assemblages between homogeneous and heterogeneous crop fields, in the different study regions in South Africa, and (iv) to test whether it is possible to implement management strategies in a seed potato agro-ecosystem inferred from an experimental study conducted in a different region.

The Pretoria study was designed to evaluate aphid host plant preferences for the five crops compared, to select a crop that could be used as a crop border plant that is preferred by aphids. The Christiana study was undertaken to determine aphid landing rates in potato fields. It was not possible to carry out the Pretoria trial in Christiana due to logistical constraints.

4.2 Materials and methods

4.2.1 Study sites – Pretoria and Christiana

Five crops, potato (*Solanum tuberosum* L., Solanaceae, 'BP1'), lucerne (*Medicago sativa* L., Fabaceae, 'Standaard'), wheat (*Triticum aestivum* L., Gramineae, 'Kariega'), maize (*Zea maize* L., Gramineae, 'CRN 3505') and soybean (*Glycine max* (L.) Merr., Fabaceae, 'Moekwa') were planted in a randomized block design at the University of Pretoria Experimental Farm (Pretoria, South Africa, 25º43'S 28º17'E) in March 2006 (Fig. 3.1). The crops were selected based on previous discussions with potato growers. The four crops selected are non-host plants of PVY (DiFonzo *et al*., 1996; Pers. Comm. K. Krüger) A field (20 x 75 m) was subdivided into six blocks, each containing five 5 x 5 m plots with 1 m fallow ground between plots. Within each block five crops were randomly assigned to one of the five plots. Each plot contained 11 rows of plants. Potato tubers were planted 60 cm apart, and seeds of maize and soybean sown 20 cm apart. Wheat and lucerne were sown evenly within each row. The distances were selected to ensure an even coverage of the surface area of a plot with plant foliage as far as possible. Crops were fertilized and irrigated according to normal farming practices. No pesticides were applied to the crops during the trial. The crops were naturally infested by aphids.

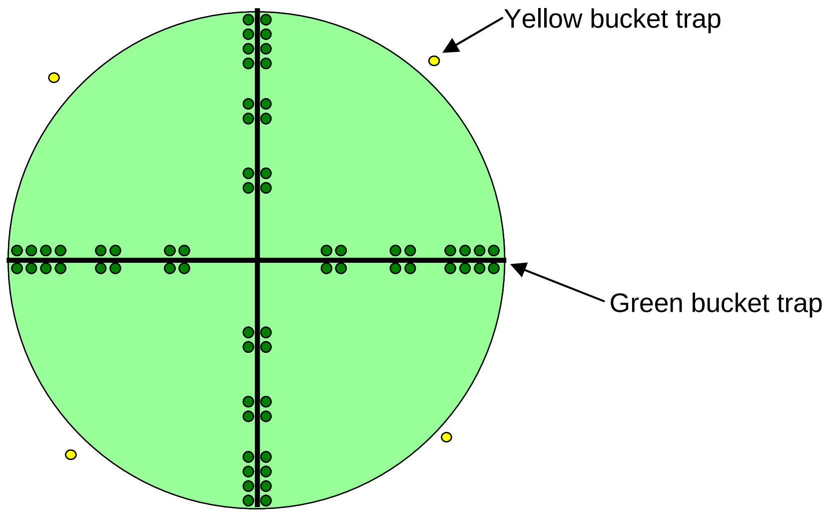
Three circular fields were planted with seed potato tubers in the Christiana seed potato production region of South Africa in January 2006. The three fields differed in size and in the crops growing adjacent to the fields. Field 1 (S 27° 3’29’’ E 25° 9’73’’), 40 ha in size, had lucerne and maize growing on the northern and southern side of the field, respectively. Field 2 (S 28° 3’29’’ E 25° 8’51’’) 30 ha in size, had a maize field growing on the southern side. The smallest field, Field 3 (S 28° 9’73’’ E 25° 12’55’’) with 20 ha, had no other crops growing in the immediate vicinity. The potato crops were fertilized, irrigated and treated with insecticides according to standard seed potato production practices in the region. Aphids naturally occurring in the three sites were sampled.

4.2.2 Aphid sampling

Green plastic bucket traps (35 cm x 10 cm), filled with water and liquid detergent added to break surface tension, were used to sample alatae aphids landing in the crops in Pretoria and seed potato fields in Christiana. Green was selected for the bucket traps as it resembles the foliage of the crops and is considered to give an unbiased estimate of aphid abundance and species composition within plots and fields (Döring *et al.*, 2004; Hodgson & Elbakhiet, 1985; Basky, 2002). The green bucket traps had a hole covered with gauze just below the upper rim to avoid overflowing from rain and irrigation water. The traps were kept at canopy level of the respective crops throughout both trials. The content of the green bucket traps was emptied into jars containing 70 % ethanol in weekly intervals.

Fig. 4.1. Single green plastic bucket trap in the centre of a plot in Pretoria.

A single green bucket trap was placed in the centre of each of the 5 x 5 m plots in Pretoria (Fig. 4.1). Aphid collection commenced on the 19th of April 2006 and was terminated on the 25th of May 2006 due to frost setting in. In Christiana four transects of 16 green bucket traps were placed in a cross-formation in each field. Each transect consisted of four groups of two traps at the edge of the field, at 2, 7, 12 & 17 m into the field, and four groups of two traps placed at 117, 122, 222 & 277 m from the edge towards the centre of the field. The two traps forming a group were placed 5 m apart (Fig 4.2). Four yellow bucket traps, which did not form part of this study, were placed around each field for aphid monitoring.



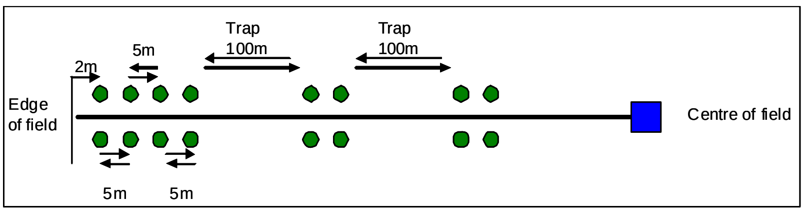


Fig. 4.2. Sampling design of a field for the Christiana trial. Four transects of green bucket traps placed in an cross-formation in three seed potato fields each.

4.2.3 Aphid identification

Aphids collected from the green bucket traps were sorted, counted and the alatae were identified by M.L. Fourie (Pretoria & Christiana) and L. Muller (Christiana) to species level with the exception of damaged individuals. *Sitobion* spp. and *Aphis* spp. were identified up to species level where possible. Individuals belonging to these genera that could not be identified to species level were grouped together. Aphid species identifications were verified by I. Millar of the Biosystematics Division of the ARC-Plant Protection Research Institute (ARC-PPRI).

4.2.4 Statistical analysis

Sampling efficiency was evaluated by compiling sample-based rarefaction curves (species accumulation curves; Gotelli & Colwell, 2001), which describe the relationship between sampling effort and sampling success, separately for each region. The data were pooled over weeks and traps were analyzed, applying a presence-absence transformation. The total number observed species for each trap (sample unit) was compared with the number of observed species sampled from each crop and site, respectively, for Pretoria and Christiana. The species richness curve stabilizes (reaches an asymptote) at a particular number of samples, indicating that observed species richness is independent of sample size at the point where the curve stabilizes. The point where the asymptote is reached corresponds to the minimum number of samples needed to estimate species richness adequately (Longino *et al.*, 2002). Sampling adequacy was determined by calculating the Chao 1 species richness estimate using EstimateS (Version 7.5, Colwell, 2005). The Chao 1 estimate computed with abundance data is not sensitive to sample size and is recommended for instances of comparing different sample size and small sampling units, such as traps (Hortal *et al.*, 2006). If the maximum species richness estimate converges with the maximum observed richness value, sampling is considered to be adequate (Longino *et al.*, 2002).

Multidimensional scaling (MDS) ordinations were computed using PRIMER (Primer 5 version 5.2.9 Clark & Warwick, 2001) to compare aphid species assemblages between the three fields at Christiana and the five crops at Pretoria. The MDS configurations of the samples were computed from similarity matrices based on the Bray-Curtis similarity index:

$$S_{jk} = 100 \frac{\sum_{i=1}^{p} 2\min(y_{ij}, y_{jk})}{\sum_{i=1}^{p} (y_{ij} + y_{jk})} \qquad (1)$$

The samples with the highest similarity are plotted closest to each other on the ordination plot. The stress value computed by the MDS analysis is a measure of goodness of fit. A good representation is characterized by stress < 0.05 (Clarke & Warwick, 2001). Analysis of Similarity (ANOSIM) can be used to determine which species are responsible for the main differences between aphid species assemblage among the fields and crops, respectively. However, the groups compared in the present study were too small to run the test.

The percentage of species shared between the two regions was determined by the Sørenson index:

$$S = 2A/2A + B + C \qquad (2)$$

where A is the number of species shared, B is the number of species unique to Pretoria and C is the number of species unique to Christiana. The number of species shared between the regions was compared based on presence/absence data, giving equal statistical weight to rare and common species (Chao *et al.*, 2005).

Similarity between the two regions was compared by subtracting the percentage of dissimilarity from 100, determined by the analysis of similarity percentages (SIMPER) using PRIMER. Dissimilarity between the two regions can be broken down into separate species contributions, termed discriminating species. A good discriminating species is to have a large average dissimilarity ($\bar{\delta}$) to standard deviation [SD ($\bar{\delta}$)] ratio. The average dissimilarity as computed by the Bray-Curtis dissimilarity index,

$$\bar{\delta}_{jk(i)} = 100.\left| y_{ij} - y_{ik} / \sum i = j \sum_{i=j}^{p} (y_{ij} + y_{ik}) \right. \qquad (3)$$

first computes the average dissimilarity between groups (sites or crops and Christiana and Pretoria), then breaks this dissimilarity down, into separate contributions of each species to the average dissimilarity ($\bar{\delta}$). The standard deviation of the average dissimilarity (SD ($\bar{\delta}$)) is a measure of the consistency of the contribution of a species to the average dissimilarity ($\bar{\delta}$) across all pairs of samples (Clarke & Warwick, 2001). With the SIMPER analysis, the average contribution of a species to the average similarity ($\bar{S}$) within a group can be determined in the same way. A species that is typifying of a group is to have a high average similarity ($\bar{S}$) to standard deviation [SD ($\bar{S}$)] ratio. The more abundant a species, the more it will contribute to the average similarity ($\bar{S}$). However, typifying species should not be used to discriminate between groups, as the average similarity is a measure of within group similarity and not between groups. Thus, it identifies the common species contributing to the within group similarity of Pretoria and Christiana separately; it does not compare similarity between Pretoria and Christiana (Clarke & Warwick, 2001).

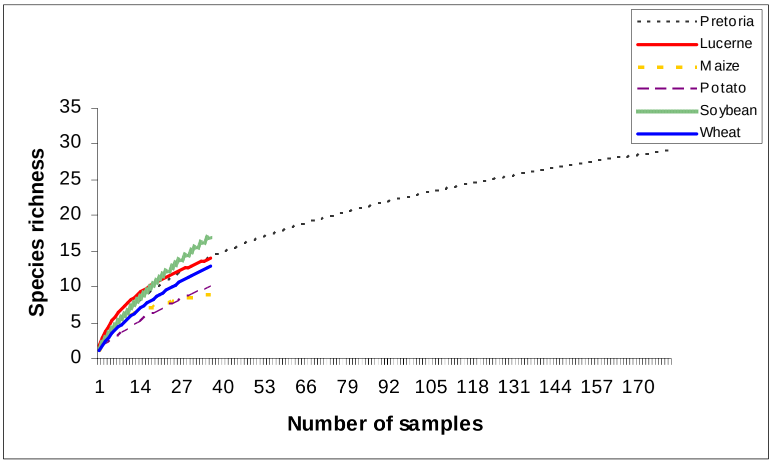
4.3 Results

A total of 495 aphids were collected from the green bucket traps placed in the five crops in Pretoria, and 6447 from the three sites at Christiana over the six- and five-week collecting periods, respectively. Thirty-two species were identified from Pretoria and 38 species from Christiana, belonging to three subfamilies of the Aphididae. From Pretoria, 26 species belonged to the subfamily Aphidinae, four species to Drepanosiphinae and two species to Pemphiginae. Similarly, the highest number of 33 species found in Christiana belonged to the subfamily Aphidinae, three species to Pemphiginae and two species to Drepanosiphinae.

Sample-based species rarefaction curves did not reach an asymptote for Pretoria, the different crops sampled, as well as the Christiana region and the different fields. This indicates, that aphid species assemblages sampled in the crop fields were underestimated for both regions (Fig. 4.3).

The maximum observed species richness and the maximum estimated species richness for Pretoria (all crops pooled), Christiana (all sites pooled), and the different crops sampled in Pretoria and the different sites in Christiana differed considerably, except for Field 1 (Table 4.1). Estimated species richness for Field 1 is thus considered representative of the aphid species assemblage landing in the potato field, but not for the other two fields in Christiana. The aphid species richness for Pretoria and the five crops sampled were thus undersampled.

a



b

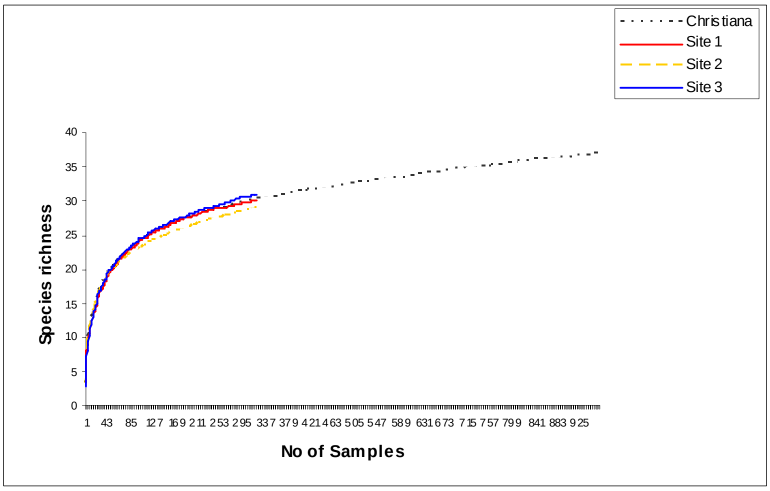


Figure 4.3. Sample-based species rarefaction curves of aphid assemblages at Pretoria (a) and Christiana (b).

Differences in aphid species assemblages between the different crops were small. Multi-dimensional scaling (MDS) ordination (Fig. 4.4a) indicates species overlap between lucerne, potato, soybean, and wheat. Species composition and abundance on maize differed from lucerne and potato and showed an overlap with wheat. The three fields at Christiana did not differ with regard to aphid species composition and abundance (Fig 4.4b) and the data for both regions were pooled for subsequent analyses.

Table 4.1. The maximum number of observed species (Sobs) in the pooled samples and the Chao1 species richness estimator.

Site	Sobs	Chao 1	± SD
Pretoria	29	39.08	± 8.00
Lucerne	14	32.00	± 23.62
Maize	9	12.00	± 4.48
Potato	10	16.00	± 6.48
Soybean	17	53.00	± 33.41
Wheat	13	45.00	± 39.60
Christiana	37	53.00	± 16.49
Site 1	30	32.00	± 2.65
Site 2	29	38.00	± 10.17
Site 3	31	55.50	± 31.11

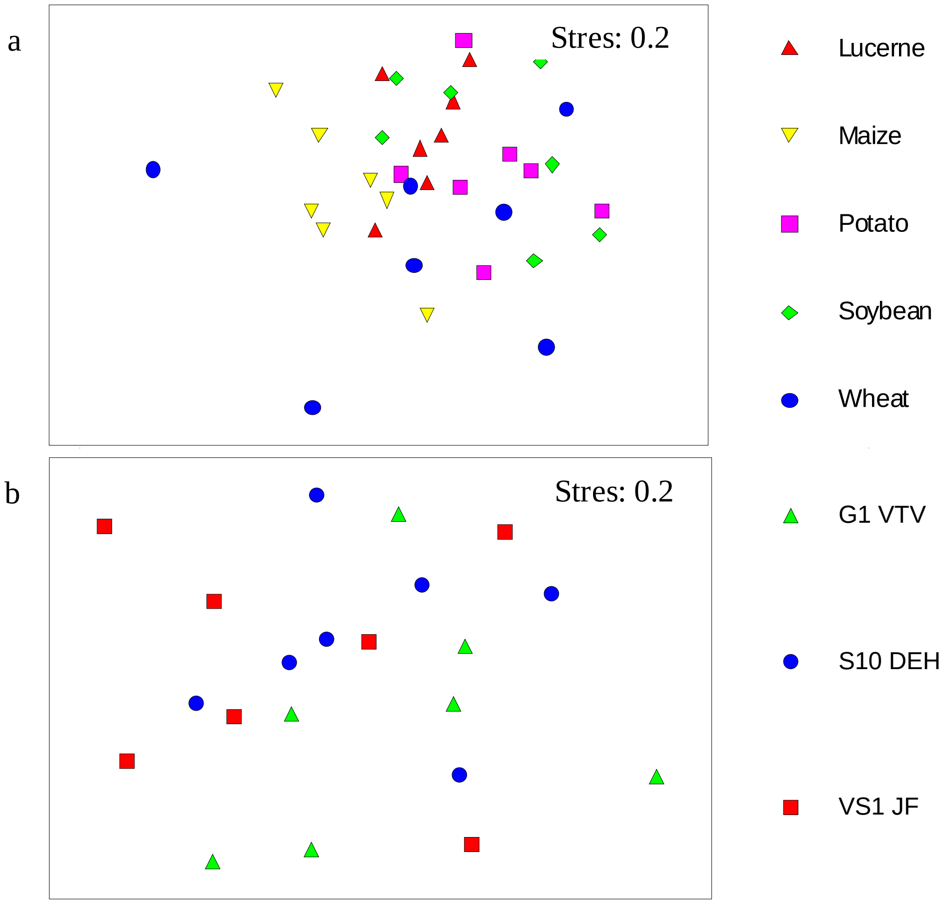


Figure 4.4. Multi-dimensional scaling (MDS) ordination of aphid species assemblage collected from five different crops in Pretoria (a) and three different seed potato fields in Christiana (b).

Overall aphid species overlap between Pretoria and Christiana based on presence/absence was relatively high (Sørenson index = 0.59). However, when determining percentage similarity based on the Bray-Curtis coefficient, taking richness and abundance into consideration, the similarity between the two regions was lower (mean similarity = 43.29 %). The highest species overlap was found between the three sites in Christiana (Table 4.2). For crops, lucerne had the highest species overlap with the other crops in Pretoria as well as the three fields in Christiana, followed by soybean and wheat (Table 4.2). Percentage similarity for aphid species between the crops in Pretoria was low for all combinations (Table 4.3). In accordance with the species overlap, lucerne was most similar to the fields in Christiana, although the percentage of similarity was relatively low and of similar magnitude to the oher crops. The percentage of similarity between maize, potato, soybean and wheat to the Christiana fields were of similar magnitude (Table 4.3).

Table 4.2. Sørenson's index of species similarity between crops and fields at Pretoria and Christiana, respectively.

	Field 1	Field 2	Field 3	Lucerne	Maize	Potato	Soybean
Field 2	0.85						
Field 3	0.89	0.84					
Lucerne	0.58	0.51	0.53				
Maize	0.39	0.3	0.38	0.67			
Potato	0.43	0.39	0.42	0.61	0.39		
Soybean	0.56	0.45	0.55	0.72	0.55	0.57	
Wheat	0.44	0.44	0.38	0.63	0.32	0.45	0.47

Table 4.3. Percentage similarity determined by SIMPER between crops and fields at Pretoria and Christiana, respectively.

	Field 1	Field 2	Field 3	Lucerne	Maize	Potato	Soybean
Field 2	68.83						
Field 3	67.02	70.12					
Lucerne	33.9	34.15	34.67				
Maize	25.08	24.77	26.56	34.96			
Potato	22.29	22.64	24.25	43.85	32.27		
Soybean	22.23	22.34	24.56	38.37	26.17	45.64	
Wheat	26.37	26.37	27.46	39.12	34.55	41.55	32.99

The species responsible for the difference in aphid species assemblages between Pretoria and Christiana are *Lipaphis pseudobrassicae* (Kaltenbach), *Schizaphis graminum* (Rondani), *Sitobion africanum* (Hille Ris Lambers) and *Acyrthosiphon* spp. (Table 4.4). These species were not recorded in Pretoria. *Aphis fabae* (Scopoli), and

Myzocallis castanicola (Baker), on the other hand, were only collected in Pretoria, although at very low numbers, and contributed much less to the dissimilarity than the species only collected from Christiana. The remaining species contributing to the dissimilarity were collected from both regions, although in much higher numbers from Christiana than Pretoria, with the exception of *Macrosiphum euphorbiae* (Thomas), which was most abundant in Pretoria. *Rhopalosiphum padi* (Linnaeus) and *Tetraneura fusiformis* (Sasaki) were the two most abundant species, thus typifying species, for both Pretoria & Christiana (Tables 4.5, 4.6). *Lipaphis pseudobrassicae*, *A. fabae*, *M. euphorbiae*, and *R. padi* are known PVY vectors. The vector status of the other discriminating species is presently unknown (Table 4.7).

Table 4.4. Species discriminating between Christiana and Pretoria, at the 50 % cut-off point (Diss = dissimilarity, SD = standard deviation).

Aphis species	Diss/SD	% Contribution	Cumulative %
Aphis spp.	2.29	5.05	5.05
Therioaphis trifolii	1.79	4.65	9.7
Acyrthosiphon spp.	7.07	4.22	13.92
Acyrthosiphon pisum	1.74	3.88	17.8
Rhopalosiphum maidis	1.87	3.81	21.62
Macrosiphum euphorbiae	1.5	3.73	25.35
Aphis fabae	1.78	3.62	28.97
Sitobion africanum	8.35	3.41	32.37
Hysteroneura setariae	2.34	3.3	35.67
Lipahis pseudobrassicae	11.19	3.25	38.92
Rhopalosiphum nymphaeae	2.21	3.14	42.05
Schizaphis graminum	8.94	3.03	45.08
Aphis nerii	2.54	2.85	47.94
Myzocallis castanicola	1.92	2.84	50.77

Table 4.5. Typifying species for the Christiana region at the 50 % cut-off point.

Aphid species	Average Similarity	% Contribution	Cumulative %
Rhoaplosiphum padi	6.62	7.74	7.74
Tetraneura fusiformis	6.5	7.61	15.35
Aphis spp.	5.92	6.93	22.28
Therioaphis trifolii	5.75	6.73	29.01
Acyrthosiphon pisum	5.08	5.95	34.96
Rhopalosiphum maidis	4.61	5.39	40.35
Acyrthosiphon kondoi	3.87	4.53	44.88
Acyrthosiphon spp.	3.64	4.26	49.13
Hysteroneura setariae	3.53	4.12	53.26

Table 4.6. Typifying species for the Pretoria region at the 50 % cut-off point.

Aphid species	Average Similarity	% Contribution	Cumulative %
Tetraneura fusiformis	12.02	22.86	22.86
Rhopalosiphum padi	6.44	12.25	35.11
Sitobion spp.	6.07	11.53	46.65
Macrosiphum euphorbiae	3.72	7.07	53.72

Table 4.7. Aphid species collected in green bucket traps at Pretoria and Christiana and their PVY vector status. Vector status from Ragsdale *et al.* (2001) and Radcliffe (1982).

Aphid species	Number of individuals Christiana	Number of individuals Pretoria	PVY vector
Acyrthosiphon kondoi	126	26	
Acyrthosiphon pisum	407	26	+
Acyrthosiphon spp.	148	0	
Aphis craccivora	8	2	+
Aphis fabae	0	14	+
Aphis gossypii	7	2	+
Aphis nerii	51	3	
Aphis oenotherae	3	0	
Aphis pseudocardui	1	0	
Aphis spiraecola	7	3	+
Aphis spp.	1261	3	+
Brachycaudus spp.	0	1	
Brachycaudus helichrysi	1	0	+
Capitophorus hippophaes	11	0	+
Coloradoa rufomaculata	2	0	
Dysphasia spp.	0	1	+
Eriosoma lanigerum	1	1	
Geoica lucifuga	17	0	
Hyadaphis spp.	1	0	
Hyalopterus pruni	9	0	+
Hyperomyzus carduellinus	2	0	
Hyperomyzus lactucae	2	3	+
Hysteroneura setariae	103	1	
Lipaphis pseudobrassicae	48	29	+
Macrosiphum euphorbiae	2	0	+
Melanaphis sacchari	15	0	
Metopolophium dirhodum	25	19	+
Mycromyzus spp.	0	3	
Myzocallis castanicola	0	5	
Myzus ornatus	1	0	not reported
Myzus persicae	2	7	+
Neotoxoptera oliveri	0	2	
Pemphigus populitransversus	20	0	
Paoliella spp.	0	1	
Rhopalosiphum maidis	336	2	not reported
Rhopalosiphum nymphaeae	92	1	
Rhopalosiphum padi	1064	29	+
Rhopalosiphum rufiabdominalis	18	1	
Rhopalosiphum spp.	1	0	

Table 4.7 continued

Aphid species	Number of individuals Christiana	Number of individuals Pretoria	PVY vector
Saltusaphis scirpus	20	2	
Schizaphis graminum	37	0	not reported
Schizaphis spp.	0	1	
Sitobion africanum	57	0	
Sitobion avenae	0	1	+
Sitobion fragariae	0	1	+
Sitobion spp.	92	15	not reported
Tetraneura fusiformis	1205	283	
Therioaphis trifolii	1244	6	
Uroleuchon sonchi	0	1	

4.4 Discussion

The resource concentration hypothesis (Root, 1973) states that insect herbivores will occur in higher abundance in habitat patches containing high densities of host plants. The findings of this study, i.e. increased aphid abundance and species richness in a monoculture, seem to be in accordance with this hypothesis in support of previous studies. The monoculture fields at Christiana ranged from 20 – 40 ha fields whereas the polyculture field at Pretoria was only 0.15 ha. Cai *et al*. (2007) reported an increased species richness of the herbivorous community occurring in Chinese cabbage fields. Favret and Voegtlin (2001) observed a higher number of migrating alatae aphids landing in soybean crop fields than in natural vegetation. However, the relationship between patch size and abundance as predicted by the resource concentration hypothesis differs between taxa (Grez & Gonzalez, 1995). The relationship between patch size and density may be affected by the dispersal ability of the organism or host plant searching behaviour (Kareiva, 1985; Grez & Gonzalez, 1995; Buckovinszky *et al*., 2005). Organisms with low dispersal ability are more likely to locate and stay in large patches. The density of insects with high dispersal ability, such as aphids, is independent of patch size (Grez & Gonzalez, 1995). Buckovinszky *et al*. (2005) found that background vegetation altered the relationship between Brussel sprout patch size and density of the cabbage aphid *Brevicoryne brassicae* (L.) and the diamondback moth *Plutella xylostella* (L.), possibly by physically masking the Brussel sprouts, in addition, the increase in structural complexity could alter host plant acceptance. Therefore, it is likely that other mechanisms were involved in the difference in aphid species richness, abundance and composition observed during the present study. Other plant characteristics such as physical obstruction caused by plant height (Javaid & Joshi, 1995; Ofuya, 1997), visual camouflage of the host plant (Irwin *et al*., 2000; Saucke & Döring, 2004), and plant volatiles attracting or repelling aphids (Picket *et al*., 1997; Quiroz *et al*., 1997; Hori 1998) could have impeded the ability of the aphid to locate a potential host plant in the polyculture planted at Pretoria.

Differences in aphid species composition between the two sites could further be attributed to the difference in structure and composition of the vegetation surrounding the potato fields and crops in Christiana and Pretoria, respectively. Habitat type was the most important factor explaining differences in species composition of plants, butterflies and carabid beetles between cereal fields, leys and semi-natural pastures (Weibull & Östman, 2003). The study conducted in Pretoria was on an Experimental Farm in the city with intense human activities, surrounded by roads and structured gardens. The study undertaken in Christiana was in a farming landscape consisting of large monoculture fields surrounded by fallow ground with patches of natural vegetation in between. The two most abundant species found in both regions, *Rhopalosiphum padi* and *Tetraneura fusiformis*, feed on Poaceae. Host plants listed for *R. padi* include cereals such as maize and wheat and for *T. fusiformis* include grasses such as *Eragrostis* spp., *Paspalum dilatatum*, *Pennisetum clandestinum* and *Sorghum vulgare* (Millar & Dürr, 1985). Cereal fields and grass pastures are characteristic of the landscape in both regions. It is unclear why *Sitobion africanum*, *Schizaphis graminum* and *Lipaphis pseudobrassicae* were only collected at Christiana. It is possible that these aphid species alighted on potato due to a limited availability of their host plant. Both *Sitobion africanum* and *Schizaphis graminum* feed on Poaceae, and *L. pseudobrassicae* on Brassicaceae (Millar & Dürr, 1985). *Sitobion africanum* and *Schizaphis graminum* are known to be widely distributed throughout Africa and *Lipaphis pseudobrassicae* worldwide (Millar, 1990). The apparent absence of *Aphis fabae* in Christiana could have been due to grouping of the *Aphis* species at the genus level. In addition, it is a highly polyphagous species distributed globally (Millar & Dürr, 1985; Millar, 1990). Similar, the absence of *Acyrthosiphon* spp. in Pretoria could be because these individuals were only identified up to the genus level. These individuals could be species present in both regions. *Myzocallis castanicola*, thought to originate from Europe, has been recorded on English oak, *Quercus robur* (Fagaceae), in South Africa (Millar & Dürr, 1985). It is likely that the presence of this species in Pretoria can be attributed to the abundance of gardens in the region. I, therefore, conclude that the difference in species overlap could have been a matter of under sampling and the difference in percentage of similarity between the two regions due to the difference in surrounding landscape structure.

Aphids generally have a high degree in host plant specificity; only 5% of species are considered to be polyphagous (Millar, 1990; Blackman & Eastop, 2000). It is well established that aphids respond to visual and olfactory cues during the initial stages of host plant searching (Powell *et al*., 2006). Therefore, it would be expected that aphids respond strongly to these cues and will only alight on their host plants. However, it is the non-colonizing aphid species that are largely responsible for spreading non-persistent viruses in crops, such as PVY in potatoes (Summers *et al*., 1990; DiFonzo *et al*., 1996; Fereres, 2000). This is due to aphids responding to the edge effect created by the contrast between the green colour of the crop and the fallow ground surrounding it (DiFonzo *et al*., 1996; Fereres, 2000; Hooks & Ferreres, 2006). After landing on a plant, the second phase, contact evaluation, of host plant searching will commence. As a tarsal contact reflex the aphids will insert their stylets into the plant and ingest small amounts of leaf sap before accepting or rejecting the plant (Caillaud, 1999; Powell & Hardie, 2000; Powell *et al*., 2006;). The planting of a crop border displaces the edge of the field, thus reducing the number of immigrating aphids landing on the main crop. The aphids purge their mouthparts on the border crop before moving into the field proper. By utilizing a crop that is a virus non-host and preferred by aphids, the border effect could be strengthened, thus increasing virus control (DiFonzo *et al*., 1996; Fereres, 2000; Ragsdale *et al*., 2001; Radcliffe & Ragsdale, 2002; Nault *et al*., 2004; Hooks & Fereres, 2006). The study conducted in Pretoria was initially designed to identify a crop that is preferred by aphids to use as a crop border plant. It is concluded that maize and wheat has the most potential to be used as border plants based on aphid species composition and abundance on the different crops. Among the typifying species recorded at Christiana, *R. padi*, *T. fusiformis*, *R. maidis*, *A. kondoi* and *H. setariae* are known to utilize Poaceae as host plants, but not Solanaceae. Therefore, it is possible to implement management decisions made from the study in Pretoria in a seed potato production system, such as that at Christiana. Further, the crop border will contribute to diversification of the crop, possibly leading to a reduction in aphid numbers on potato due to most of the aphid species landing in the potato fields at Christiana not colonizing potatoes (Millar & Dürr, 1985).

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Chapter 5

General discussion

Trap crops are broadly defined as plant stands that attract, divert, intercept and/or reduce damage to the main crop (Shelton & Badenes-Perez, 2006). They form part of ecological, environmentally-friendly pest management strategies aimed at habitat manipulation of agro-ecosystems (Benton *et al*., 2003; Hooks & Fereres, 2006). Viewing trap cropping in the context of landscape ecology, crop borders can contribute to restoring agro-ecosystem stability. This in turn would decrease aphid numbers and species richness in seed potato fields by reducing the percentage of land covered by monocultures (Altieri & Letourneau, 1982). A more diverse environment increases the availability of possible food and habitat resources, decreasing the likelihood of PVY spread into potato fields (Altieri, 1999).

In the current study, the attractiveness of lucerne, maize, soybean and wheat to potato colonizing and non-colonizing aphids, in comparison to potato, was determined. Based on aphid species composition and abundance, including potato colonizing and non-colonizing aphid species, maize and wheat were the most suitable crops of those tested. The selection of a crop border plant, such as maize or wheat, preferred by aphids over potato as a food resource, combines two management strategies, trap cropping as well as crop borders, to reduce non-persistently aphid transmitted viruses (Hokkanen, 1991; Hooks & Fereres, 2006). Trap crops attract aphids and provide additional arresting cues, increasing the likelihood of aphids feeding on the border crop for longer periods, before moving into the crop (Shelton & Badenes-Perez, 2006). In addition, the crop plants identified in the present study are virus non-hosts acting as a virus sink. The combination of these mechanisms strengthens edge effects, improving the effectiveness of crop border plants in reducing non-persistently transmitted viruses by aphids.

The use of a preferred crop as a border plant may lead to aggregation of aphids, causing the border crop to act as an aphid source. It is, however, possible to control aphid population numbers by applying therapeutic control methods, such as insecticides and mineral oil sprays to the border crop (Hokkanen, 1991; Radcliffe & Ragsdale, 2002). Efficient suppression of aphid numbers in border crops may lead to a reduction in the number of preventative insecticide applications to the potato crop reducing production costs (Hokkanen, 1991). Further, aphids leaving border plants and entering the main crop are likely to be virus free after initial probing of the border crop plants (DiFonzo *et al*., 1996; Fereres, 2000).

An additional aim was to determine if the crop border plant(s) selected could be implemented in a seed potato production area comparing alatae species composition and abundance of alatae alighting in the fields. Based on species composition and number of non-colonizing species and PVY vectors, maize and wheat could be used as a trap crop planted as a border crop in a seed production region such as Christiana. Further, the economic implications of crop borders should be considered before including it in non-persistent virus management programmes. The area of land needed for the crop border plays an important role. This reduces the land available for primary production and subsequently seed potato yields. Therefore, a crop border would only be suitable for high value cash crops such as seed potatoes, and not for ware potato production (Hokanenen, 1991; Shelton & Badenes-Perez, 2006). The percentage of virus tolerated for ware potatoes is much lower than for seed potatoes, causing the risk of PVY to be greater for seed potato growers (Hane & Humm, 1999). Given the economic implications of planting a crop border around seed potatoes, it is advantageous to select a crop that is compatible with current production practices (Ragsdale, *et al*., 2001). Maize and wheat are grown in the Christiana region and are therefore compatible with the production practices in this region.

Future research should determine the efficiency of the most abundant aphid species in transmitting PVY in the seed potato production regions of South Africa, such as *Tetraneura fusiformis*. This species is of particular interest as it is a root feeding aphid and has not been reported to colonize potatoes. However, the present study indicates that it prefers potato over maize, which belongs to the Poaceae from which it has been recorded (Millar & Dürr, 1985). Before crop borders can be implemented in seed potato production regions of South Africa, their efficiency in reducing both aphid numbers landing in potatoes and incidence of non-persistently transmitted viruses, e.g. PVY, in potato fields has to be determined.

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Appendix A. Classification of the aphids of South Africa followed in the present study (Millar, 1990). Species identified in the present study are marked with an asterisk.

Superfamily: Aphidoidea
Family: Adelgidae
Pineus Shimer, 1869
P. pini (Macquert, 1819)
Family: Phylloxeridae
Moritziella Börner, 1908
M. corticalis (Kaltenbach, 1867)
Viteus Shimer, 1867
V. vitifoliae (Fitch, 1855)
Family: Aphididae
Subfamily: Lachninae
Tribe: Cinarini
Cedrobium Remaudière, 1954
C. laportei Remaudière, 1954
Cinara Curtis, 1835
C. cronartii Tissot & Pepper, 1967
C. tujafilina (Del Guercio, 1909)
Eulachnus Del Guercio, 1909
E. rileyi (Williams, 1911)
Tribe: Lachnini
Tuberolachnus Mordvilko, 1909
T. salignus (Gmelin, 1790)
Subfamily: Chaitophorinae
Tribe: Chaitophorini
Chaitophorus Koch, 1854
C. leucomelas Koch, 1854
C. populialbae (Boyer de Fonscolombe, 1841)
Tribe: Siphini
Sipha Passerini, 1860

S. (*Rungsia*) *maydis* (Passerini, 1860)

Subfamily: Drepanosiphinae

Monelliopsis Richards, 1965

M. pecanis Bissell, 1983

Myzocallis Passerini, 1860

M. castanicola Baker, 1917 *

Neophyllaphis Takahashi, 1920

N. grobleri Eastop, 1955

N. viridis Ilharco, 1973

Paoliella Theobald, 1928 *

P. browni Quednau, 1962

P. delottoi (Hille Ris Lambers, 1954)

P. echinata Eastop, 1956

P. nachensis (Eastop, 1955)

P. papillata (Hall, 1932)

P. terminaliae (Hall, 1932)

P. wettsteini Quednau, 1964

Saltusaphis Theobald, 1915

S. scirpus Theobald, 1915 *

Takecallis Matsumura, 1917

T. taiwanus (Takahashi, 1926)

Therioaphis Walker, 1870

T. trifolii (Monell, 1882) *

Subfamily: Geenideinae

Tribe: Cervaphidini

Eonaphis Essig, 1957

E. crotonis Quednau, 1962

Schoutedenia Rübsaamen, 1905

S. lutea Van der Goot, 1917

Subfamily: Aphidinae

Tribe: Aphidini

Subtribe: Aphidina

Aphis Linnaeus, 1758 *

A. armoraciae Cowen, 1895

A. cephalanthi Thomas, 1878

A. chloris Koch, 1854

A. craccivora Koch, 1854 *

A. (*Protaphis*) *evansi* (Eastop, 1958)

A. fabae Scopoli, 1763 *

A. gossypii Glover, 1877 *

A. hederae Kaltenbach, 1843

A. nerii Boyer de Fonscolombe, 1841 *

A. oenotherae (Oestlund, 1887) *

A. rhoicola Hille Ris Lambers, 1956

A. sedi Kaltenbach, 1843

A. spiraecola Patch, 1914 *

A. tirucallis Hill Ris Lambers, 1954

A. (*Protaphis*) *evansi* (Eastop, 1958)

A. (*P.) pseudocardui* Theobald, 1915 *

Toxoptera (Koch, 1956)

T. aurantii (Boyer de Fonscolombe, 1841)

T. citricidus (Kirkkaldy, 1907)

T. odinae (Van der Goot, 1917)

Subtribe: Rhopalsiphina

Hyalopterus Koch, 1854

H. pruni (Geoffroy, 1762) *

Hysteroneura Davis, 1919

H. setariae (Thomas, 1878) *

Melanaphis Van der Goot, 1917

M. sacchari (Zehntner, 1897) *

Rhopalosiphum Koch, 1854 *

R. maidis (Fitch, 1856) *

R. nymphaeae (Linnaeus, 1761) *

R. padi (Linnaeus, 1758) *

R. rufiabdominalis (Sasaki, 1899) *

Schizaphis Börner, 1931 *

S. graminum (Rondani, (1847) 1852) *

S. minuta (Van der Goot, 1917)

S. rotundiventris (Signoret, 1860)

Tribe: Macrosiphini

Acyrthosiphon Mordvilko, 1914 *

A. kondoi Shinji, 1938 *

A. malvae (Mosley, 1841)

A. pisum (Harris, 1776) *

Aulacorthum (Mordvilko, 1914)

A. solani (Kaltenbach, 1843) *

A. (*Neomyzus*) *circumflexum* (Buckton, 1876)

Brachycaudus Van der Goot, 1913 *

B. helichrysi (Kaltenbach, 1843) *

B. (*Acaudus*) *persicae* (Passerini, 1860)

B. (*Thuleaphis*) *amygdalinus* (Schouteden,1905)

Brevicoryne Van der Goot, 1915

B. brassicae (Linneaus, 1758)

Capitophorus Van der Goot, 1913

C. elaegni (Del Guercio, 1894)

C. hippophaes (Walker, 1852) *

Cavariella Del Guercio, 1911

C. aegopodii (Scopoli, 1763)

Chaetosiphon Mordvilko, 1914

C. (Pentatrichopus) fragaefolii (Cockerell, 1901)

C. (P.) tetrarhodum (Walker, 1849)

Coloradoa (Wilson, 1910)

C. rufomaculata (Wilson, 1908) *

Diuraphis Aizenberg, 1935

D. noxia (Mordvilko, 1913)

Dysaphis Börner, 1931 *

D. apiifolia (Theobald, 1923)

D. cynarae (Theobald, 1915)

D. foeniculus (Theobald, 1923)

D. tulipae (Boyer de Fonscolombe, 1841)

Eucarazzia Del Guercio, 1921

E. elegans (Ferrari, 1872)

Hyadaphis Kirkaldy, 1904 *

H. coriandri (Das, 1918)

H. foeniculi (Passerini, 1860)

Hyperomyzus Börner, 1933

H. carduellinus (Theobald, 1915) *

H. lactucae (Linnaeus, 1758) *

Idiopterus Davis, 1909

I. nephrelepidis Davis, 1909

Illinoia (Wilson, 1910)

I. azaleae (Mason, 1925)

Lipaphis Mordvilko, 1928

L. erysimi (*pseudobrassicae*) (Kaltenbach,1843)*

Macrosiphoniella Del Guercio, 1911

M. abrotani (Walker, 1852)

M. helichrysi Remaudière, 1952

M. sanborni (Gilette, 1908)

Macrosiphum Passerini, 1860

M. centranthi Theobald, 1915

M. euphorbiae (Thomas, 1878) *

M. rosae (Linnaeus, 1758)

Metopolophium Mordvilko, 1914

M. dirhodum (Walker, 1849) *

Microlophium Mordvilko, 1914

M. primulae (Theobald, 1913)

Micromyzella Eastop, 1955

M. pterisoides (Theobald, 1918)

M. sleonensis (Eastop, 1958)

Micromyzus Van der Goot, 1917 *

M. (*Kugegenia*) *ageni* Eastop, 1955

Myzaphis Van der Goot, 1913

M. rosarum (Kaltenbach, 1843)

Myzus Passerini, 1860

M. hemerocallis Takahashi, 1921

M. lythri (Schrank, 1801)

M. ornatus Laing, 1932 *

M. persicae (Sulzer, 1776) *

M. (*Sciamyzus*) *cymbalariae* Stroyan, 1954

Nasonovia Mordvilko, 1914

N. ribisnigri (Mosley, 1841)

Neotoxoptera Theobald, 1915

N. oliveri (Essig, 1935) *

Ovatus Van der Goot, 1913

O. crataegarius (Walker, 1850)

Pentalonia Coquerel, 1859

P. nigronervosa Coquerel, 1859

Pleotrichophorus Börner, 1930

P. chrysanthemi (Theobald, 1920)

Rhodobium Hille Ris Lambers, 1947

R. porosum (Sanderson, 1900)

Rhopalosiphoninus Baker, 1920

R. latysiphon (Davidson, 1912)

R. staphyleae (Koch, 1854)

Sitobion Mordvilko, 1914 *

S. adgnatum (Müller, 1959)

S. africanum (Hille Ris Lambers, 1954) *

S. anselliae (Hall, 1932)

S. avenae (Fabricius, 1775) *

S. cissi (Theobald, 1920)

S. colei (Eastop, 1959)

S. fragariae (Walker, 1848) *

S. graminis Takahashi, 1950

S. halli (Eastop, 1959)

S. howlandae (Eastop, 1959) *

S. nigrinectarium (Theobald, 1915)

S. ochnearum (Eastop, 1959)

S. yakini (Eastop, 1959)

Uroleucon (Mordvilko, 1914)

U. sonchi (Linneaus, 1767) *

U. (*Uromelan*) *compositae* (Teobald, 1915)

Subfamily: Anoeciinae

Anoecia Koch, 1857

A. corni (Fabricius, 1775)

Subfamily: Hormaphidinae

Tribe: Cerataphidini

Cerataphis Lichtenstein, 1882

C. orchidearum (Westwood, 1897)

C. variabilis Hill Ris Lambers, 1953

Subfamily: Pemphiginae

Tribe: Fordini

Aloephagus Essig, 1950

A. myersi Essig, 1950

Aploneura Passerini, 1863

A. lentisci (Passerini, 1856)

Geoica Hart, 1894

G. lucifuga (Zehntner, 1897) *

Smynthorodus Westwood, 1849

S. betae Westwood, 1849

Tribe: Eriosomatini

Eriosoma Leach, 1818

E. lanigerum (Hausmann, 1802) *

E. (*Schizoneura*) *lanuginosum* (Hartig, 1841)

Kaltenbachiella Schouteden, 1906

K. pallida (Haliday, 1838)

Tetraneura Hartig, 1841

T. (*Tetraneurella*) *fusiformis* (Sasaki, 1899) *

Tribe: Pemphigini

Pemphigus Hartig, 1839

P. bursarius (Linnaeus, 1758)

P. populitransversus Riley, 1879 *

Prociphilus Koch, 1857

P. fraxinifolii (Riley, 1879)

Appendix B. Aphid species and abundance recorded at the University of Pretoria Experimental Farm.

Aphid species	Leaf counts					Sweep net					Green bucket trap					
	Lucerne	Maize	Potato	Soybean	Wheat	Lucerne	Maize	Potato	Soybean	Wheat	Lucerne	Maize	Potato	Soybean	Wheat	Total
Acyrthosiphon kondoi	27					823	1	1	2	10	22		1	2	1	890
Acyrthosiphon pisum	16					415			1	3	24				2	461
Aphis craccivora									1		1			1		3
Aphis fabae		1	2		1	1					1		4	6	3	19
Aphis gossypii		1				1			1				2			5
Aphis nerii									2		1	1		1		5
Aphis spiraecola			1					1		1	1	1		1		6
Aphis spp.						1		4		2	1	1		1		10
Aulacorthum solani			3													3
Brachycaudus spp.													1			1
Dysaphis spp.															1	1
Geoica lucifuga						2			1						1	4
Hyperomyzus lactucae				1									1	2		4
Hysteroneura setariae					1	1				1			1			4
Macrosiphum euphorbiae	15	472	58		5		4	24	3	4	3	20	4	2		614
Melanaphis sacchari										1						1
Metapolophium dirhodum	13	222		1	74	1	5	13	1	41	1	12			6	390
Mycromyzus spp.											1	1		1		3
Myzocallis castanicola											2		1	1	1	5
Myzus ornatus							1									1
Myzus persicae			16		1		1	8	1		4		2		1	34
Neotoxoptera oliveri														1	1	2
Paoliella spp.							1						1			2
Rhopalosiphum maidis										6				1	1	8
Rhopalosiphum nymphae			1												1	2
Rhopalosiphum padi	10	168		2	18	3	18	3	3	37	6	12	2	2	7	291
Rhopalosiphum rufiabdominalis					1									1		2
Saltusaphis scirpus											1				1	2
Schyzaphis spp													1			1
Sitobion avenae		10			10									1		21
Sitobion fragariae															1	1

	Leaf counts					Sweep net					Green bucket trap					
Aphid species	Lucerne	Maize	Potato	Soybean	Wheat	Lucerne	Maize	Potato	Soybean	Wheat	Lucerne	Maize	Potato	Soybean	Wheat	Total
Sitobion howlandae		1														1
Sitobion spp.		18			5		2			34	3	3	2	2	5	74
Tetraneura fusiformis		3	2	1	1	18	11	11	11	6	73	9	97	57	47	347
Therioaphis trifolii	1					18		1			2		1	3		26
Uroleuchon sonchi												1				1
Total	82	896	83	5	117	1284	44	66	27	146	147	61	121	86	80	3245