Preference of aphids (Hemiptera: Aphididae) for lucerne, maize, soybean and wheat and their potential as prospective border crops for *Potato virus Y* management in seed potatoes

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Aphid landing rates, species composition and abundance on lucerne (*Medicago sativa*), maize (*Zea mays*), soybean (*Glycine max*), wheat (*Triticum aestivum*) and potato (*Solanum tuberosum*) were determined in a small-scale field trial to identify potential crops as prospective border plants for seed potatoes to reduce the spread of *Potato virus Y* (PVY) in South Africa. Aphids were sampled using green bucket traps to estimate aphid landing rates, whereas leaf counts and sweep-netting were used to identify colonizing species. Of the 34 species or species groups collected with green bucket traps, 18 were previously known vectors of PVY. The most abundant vector species or species groups were *Acyrthosiphon pisum*, *Macrosiphum euphorbiae*, *Metopolophium dirhodum*, *Myzus persicae*, *Rhopalosiphum padi* and *Sitobion* spp. The only other species that occurred in high numbers, but whose vector status is unknown, were *Acyrthosiphon kondoi* and *Tetraneura fusiformis.* Landing patterns suggest that *A. kondoi*, *A. pisum* and *M. dirhodum* may be able to discriminate between plant species and select their preferred host plant, if available within a habitat patch, in the pre-alighting phase, whereas other species such as *R. padi* seemed less selective. Results on aphid landing together with colonization of the crops evaluated suggest that maize and wheat show the highest potential as possible crop border plants in regions where aphids colonizing Poaceae, and lucerne in regions where aphids colonizing Fabaceae are abundant. Soybean appears to be less suitable because cultivars with a high trichome density, which reduces colonization by aphids, are preferentially planted in South Africa.

Key words: aphids, host plant preference, crop border plants, *Potato virus Y* (PVY).

INTRODUCTION

Crop borders consisting of virus non-host plants can effectively reduce the spread of non-persistently aphid-transmitted viruses such as *Potato virus Y* (PVY) (DiFonzo *et al.* 1996; Thieme *et al.* 1998; Fereres 2000). Alate (winged) adult aphids immigrating into a field are thought to react to the contrast of the brown of the fallow ground and the green of bordering plants (Moericke 1955; Kennedy *et al.* 1961), 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 proper, thus reducing the risk of non-persistent virus transmission (Fereres 2000; Hooks & Fereres 2006).

Apart from selecting a crop border plant species that is a virus non-host plant (DiFonzo *et al.* 1996; Fereres 2000), further careful consideration should be given to selecting the plant species to be used in the crop border. One aspect is the pre-alighting behaviour of aphids which may be influenced by visual and olfactory stimuli (Hooks & Fereres 2006). Some studies showed that aphids do not discriminate between host plants prior to the contact evaluation phase of leaf surface evaluation and initial leaf sap ingestion (Kennedy *et al.* 1959; Powell & Hardie 2000, Powell *et al.* 2006). However, other studies report that both visual and olfactory cues emitted by plants may influence aphid behaviour in the pre-alighting phase (Chapman *et al.* 1981; Prokopy & Owens 1983; Pickett *et al.* 1992; Pettersson *et al.* 1998; Hooks & Fereres 2006; Döring & Chittka 2007), suggesting that border crop plants should be selected to be more attractive to alighting aphids than the main crop (Hooks & Fereres 2006).

Furthermore, aphid host-plant preference in the post-alighting phase needs to be taken into account. This was demonstrated by Damicone *et al.* (2007), who observed a reduction in non-persistently aphid-transmitted viruses in pumpkin (*Cucurbita* sp., Cucurbitaceae) when planted with a grain

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sorghum (*Sorghum bicolor* (L.) Moench, Poaceae) crop border, but not when maize (*Zea mays* L., Poaceae), peanut (*Arachis hypogaea* L., Fabaceae), or soybean (*Glycine max* (L.) Merr., Fabaceae) was planted. Damicone *et al.* (2007) suggested that sorghum is a preferred host of key vector species, thus reducing take-off response of aphids after initial probing. This supports the recommendation of Nault *et al.* (2004) that a plant species preferred to the main crop by aphids as a host plant, *i.e.* post alighting, should be selected as a crop border plant.

Aphids do not always settle on and colonize the plant they initially land on (Raccah *et al.* 1985; Powell & Hardie 2000). Alates invest most of their resources in dispersal and locating host plants to start new colonies, whereas apterae (wingless aphids) will not readily move from the host plant once settled as they invest a large part of their resources in reproduction (Dixon 1977; Müller *et al.* 2001). Therefore, sampling of immigrating insects should be treated differently to that of foliar insects as the former may land on several plants before settling and reproducing (Kuno 1991). Horizontal traps, such as green bucket, tile, and flat sticky traps, provide estimates of aphid species composition and abundance of alates of colonizing and non-colonizing species in the landing phase (Hodgson & Elbakhiet 1985; Raccah *et al.* 1985; Basky 2002; Döring *et al.* 2004; Nault *et al.* 2004). Leaf counts and sweep-netting can be used to assess species composition and obtain abundance estimates of insects from plants (Southwood 1968).

Seed potato industries in many potato-growing regions throughout the world are suffering substantial economic losses due to PVY (Sigvald 1987; Omer & El-Hassan 1992; Basky 2002; Radcliffe & Ragsdale 2002; Boukhris-Bouhachem *et al.* 2007; Visser & Bellstedt 2009; Wang *et al.* 2011). The virus is transmitted non-persistently by more than 50 aphid species (Ragsdale *et al.* 2001). It is transmitted to potato fields mainly by immigrating adult alates (Radcliffe 1982) of both potato-colonizing (reproducing on potato) and non-colonizing (not reproducing on potato) species (Ragsdale *et al.* 2001). Plants become infected during short probing periods, ranging from several seconds to a few minutes, when aphids evaluate the plant sap before either continuing with probing or rejecting a plant (Fereres 2000; Powell *et al.* 2006).

The peach-potato aphid *Myzus persicae* (Sulzer), a potato-colonizing species, is considered the most efficient vector of PVY (van Harten 1983; Sigvald 1984; Verbeek *et al. 2010;* Boquel *et al.* 2011). However, non-colonizing species, such as the bird cherry-oat aphid *Rhopalosiphum padi* (L.), can contribute to high primary infection rates in seed potato fields when occurring in high numbers (van Hoof 1977; Sigvald 1987). Non-colonizing species can therefore be more important vectors than potato-colonizing species, although their transmission efficiency may be lower (van Hoof 1977; Rydén *et al.* 1983; Harrington *et al.* 1986; Sigvald 1987; Thieme *et al.* 1998; Radcliffe & Ragsdale 2002). Common vectors of PVY in many parts of the world include potato-colonizing species such as *Aphis fabae* Scopoli, *Aulacorthum solani* (Kaltenbach), *Macrosiphum euphorbiae* (Thomas) and *M. persicae,* and non-colonizing species such as *Acyrthosiphon pisum* (Harris), *Brachycaudus helichrysi* (Kaltenbach), *Metopolophium dirhodum* (Walker), *Phorodon humuli* (Schrank), *Rhopalosiphum maidis* (Fitch) and *R. padi* (Sigvald 1984; Harrington & Gibson 1989; de Bokx & Piron 1990; Sigvald & Hulle 2004; Kirchner *et al.* 2011). Several non-colonizing species that are vectors of PVY colonize Poaceae, *e.g. M. dirhodum* and *R. padi.*

Seed potatoes in South Africa are commonly planted in fields of 20–40 ha. Due to the high cost involved in testing different plant species as crop borders in an on-farm field trial directly, a small-scale field trial was undertaken to identify the most suitable plant species for further evaluation. We determined aphid-landing preference and plant colonization, using four agricultural crops. Potential plant species as prospective border plants for seed potatoes in South Africa were identified from these four crops. Aphid landing rates of alates and colonization of plant species by nymphs and adult apterae were compared between lucerne (*Medicago sativa* L., Fabaceae), maize (*Zea mays* L., Poaceae), potato (*Solanum tuberosum* L., Solanaceae), soybean (*Glycine max* (L.) Merr., Fabaceae) and wheat (*Triticum aestivum* L., Poaceae) using different collecting methods. For the purpose of this study, we define preference as a qualitative, behavioural trait that can be measured experimentally and only has meaning within the specified set of plants evaluated (Singer 2000).

MATERIAL AND METHODS

Experimental design

Four crops, lucerne (cv. 'Standaard'), maize (cv.

Fig. 1. **a**, Layout of the field trial at the Experimental Farm of the University of Pretoria; **b**, green bucket trap in the centre of a wheat plot.

'CRN 3505'), soybean (cv. 'Moekwa') and wheat (cv. 'Kariega'), were selected based on DiFonzo *et al.* (1996) and discussions with seed potato growers in South Africa. The maize and soybean cultivars were non-BT (*Bacillus thuringiensis*) cultivars. The choice of plant species was restricted to crops that are already being planted in South African seed potato growing regions because of farm management practices.

To compare aphid landing preferences, species composition and abundance of the four potential border crops and potato (cv. 'BP1'), the five crops were planted in a randomized block design at the Experimental Farm of the University of Pretoria (Pretoria, South Africa, 25°43′S 28°17′E) (Fig. 1a) on 8 March 2006. A field was subdivided into six blocks. Within each block the five crops were randomly assigned to each of five 5 × 5 m plots with 1 m fallow ground around each plot as a buffer zone. The design was chosen so that each crop has the same chance of aphid landing and colonization in order to avoid bias for any given crop. Each plot contained 11 rows of plants. Within a row 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 as even a coverage of the surface area within a plot with plant foliage as far as possible. Potatoes were pre-sprouted. Seeds, treated with fungicides, were sown, but no insecticides were applied to the crops during the trial. Crops were fertilized and irrigated according to normal farming practices. The crops were naturally infested by aphids.

Aphid sampling and identification

Aphid abundance, landing rates of alate adult aphids and species colonizing the crops were determined using three collection methods. Green bucket traps (Induspol Plastics cc, South Africa) were used to estimate aphid landing rates. The highest reflection (7 %) occurred at 520 nm (AvaSpec-3648, Avantes, the Netherlands). Green traps instead of yellow traps were used to resemble the wave reflectance of plant foliage and obtain an unbiased estimate of aphid landing rates (Irwin 1980). A single green plastic bucket trap (35 cm diameter, 10 cm height), filled to 5 cm with water and with *c.* 7 ml liquid detergent added, was placed on customized metal stands with central poles in the centre of each plot (Fig. 1b). To avoid overflow from rain and irrigation water the green bucket traps had a hole covered with gauze just below the upper rim. The depth of the poles of the trap stands in the soil was adjusted according to plant height throughout the trial, so that the rim of the green bucket traps was kept at canopy level of the respective crops. To avoid sampling bias caused by a specific method due to plant architecture and aphid behaviour, leaf counts and sweep-netting were used to identify colonizing aphid species. For leaf counts, 10 plants were randomly selected within each plot and the number of aphids found on four top, middle and bottom leaves each was counted. Sub-samples of aphid colonies were collected from each plant for species identification. Each week a set of 10 plants, excluding those already sampled, was randomly selected for each plot. Sweep-net samples of aphids were collected using 10 sweeps with a standardized net (32 cm diameter) across two sets of two randomly selected rows of plants per plot. Plants and rows were randomly selected using the random function in Microsoft® Office Excel 2003.

Aphid counting and collecting commenced on 19 April 2006, six weeks after planting of crops, and continued at weekly intervals for six weeks until 25 May 2006. Potatoes planted in January or February are harvested at the end of May (Daiber 1964). Aphid populations in and around Pretoria are active throughout the year. Aphids are anholocyclic in this region due to the generally mild and dry winters (Daiber & Schöll 1959). For example, highest numbers for *M. persicae* and *M. euphorbiae* occur from November to December and then again in May (Daiber 1965). However, the trial had to be terminated after six weeks of aphid sampling due to frost setting in.

Adult alates collected in green bucket traps and adult apterae and nymphs collected during leaf counts and by sweep-netting were sorted and counted. No distinction was made between alate and apterous nymphs. All adult aphids were 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 specimens belonging to these genera were grouped. Aphid species identifications were verified by I. Millar of the Biosystematics Division of the ARC-Plant Protection Research Institute (ARC-PPRI).

Statistical analysis

Total aphid abundance was analysed with linear mixed model repeated measurement analysis over six weeks using the REML procedure (Payne *et al.* 2012) in GenStat® (Payne *et al.* 2012) with a fixed model of week + crop + week × crop and plot × week as random effect. Aphid counts followed the Poisson distribution and were $\log_{10}(y + 0.5)$ transformed before analysis. To identify the species that were characteristic for aphids landing in and colonizing a crop, *i.e.* those species that contributed most to similarity within a crop and method, data were analysed with the similarity percentages (SIMPER) analysis using the Bray-Curtis similarity coefficient (Clarke 1993), with a cut-off of the cumulative percent contribution at 90 %. The data were fourth-root transformed ($Y^{0.25}$) to balance the contribution of common and rare species to the SIMPER analysis (Clarke 1993). Alate adults collected with the green bucket trap method were used to determine characteristic aphid species landing in different crops. Apterous adults of species from the leaf count and sweep-net samples were used to determine characteristic species colonizing a crop. No aphids were recorded on potato and wheat in week 16 with the leaf count method and on maize in week 18 with the sweep-net method, and both of these were excluded from the SIMPER analysis. In addition, soybean was excluded from the leaf count and sweep-net analysis due to the high number of zero counts. SIMPER was performed using PRIMER (Primer 5 version 5.2.9) (Clarke & Warwick 2001).

RESULTS

Of the 8436 aphids collected, 3245 were adults, 4972 nymphs and 219 damaged individuals that could not be identified. All undamaged alate and apterae adults collected during the trial were identified to species where possible, otherwise to species group level. Overall, 34 species or species groups were recorded. The green bucket trap samples comprised 495 alate adults and 32 species or species groups, leaf count samples contained 982 apterous adults and 9 species or species groups, and those from the sweep-net samples 1287 apterous adults and 11 species or species groups.

Aphid landing rates in green bucket traps increased in lucerne from week 19, whereas the number of aphids alighting on the other crops fluctuated between weeks (Fig. 2a, Table 1). The highest mean number of alates per crop over the six-week period was recorded in lucerne (5.6), followed by potato (3.2), soybean (2.5), wheat (2.2), and maize (1.3).

The mean number of nymphs and apterous adults recorded during the trial on leaves was similar on all crops over the sampling period except for maize and wheat (Fig. 2b, Table 1).

Aphid numbers on maize increased over the six-week period from a mean of 91.2 to 1383.5 and on wheat from a mean of 27.3 in week 18 to 117.7 in week 21. Overall, maize had the highest mean number of nymphs and apterous adults (530.7)

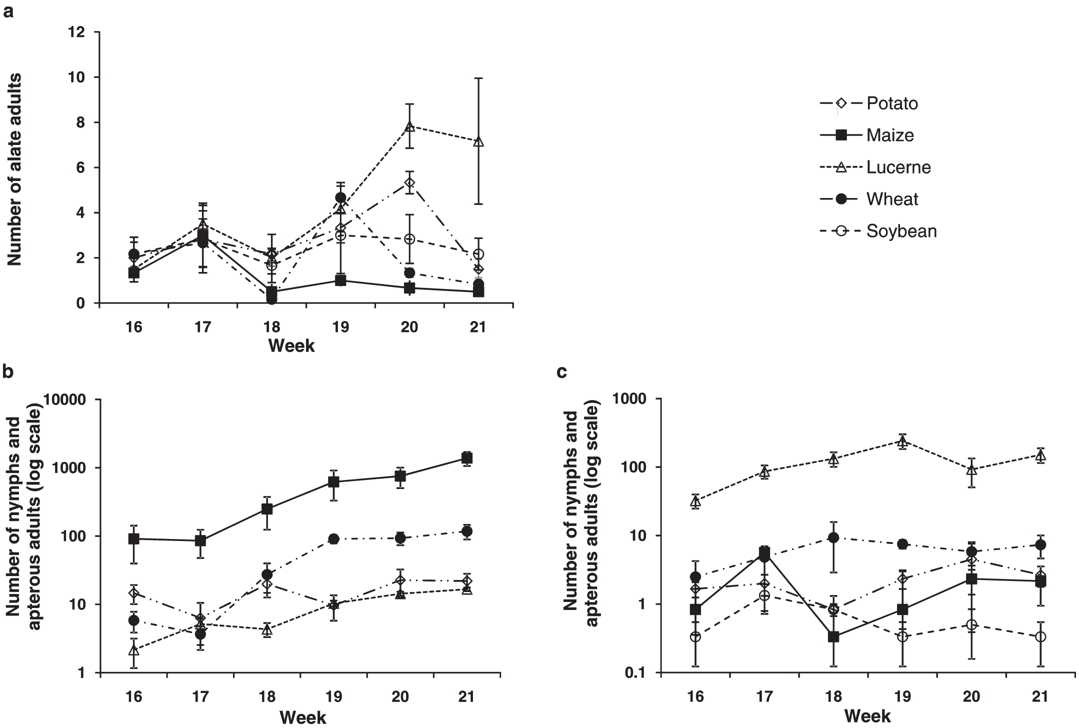

Fig. 2. Mean (± S.E.M.) number of (**a**) alate adult aphids recorded in green bucket traps, (**b**) nymphs and apterous adult aphids sampled on four top, middle and bottom leaves each, and (**c**), nymphs and apterous adults in sweep-net samples from lucerne, maize, potato, soybean and wheat over a period of six consecutive sampling weeks.

recorded on leaves, followed by wheat (56.4), potato (15.9), and lucerne (8.8). Very few nymphs and apterous adults were recorded on leaves of soybean (mean: 3.6).

Based on sweep-net sampling, the mean number of nymphs and apterous adults remained relatively constant on the different crops, except for lucerne (Fig. 2c, Table 1). In contrast to the leaf counts, lucerne had the highest mean number of aphids (123.0), followed by wheat (6.2), potato (2.3), and maize (2.0); only a few aphids were collected from soybean (mean: 0.6).

For all methods combined, eight taxa accounted for 96 % of the 2764 alate and apterous adults used for analysis of alighting and colonizing aphid species. These include the blue alfalfa aphid *Acyrthosiphon kondoi* Shinji with 811 individuals, *M. euphorbiae* (536), pea aphid *A. pisum* (424), rose-grain aphid *M. dirhodum* (303), *Tetraneura fusiformis* (Sasaki) (283), *R. padi* (219), *Sitobion* spp. (60), and *M. persicae* (26). These taxa together with *Sitobion avenae* (F.) were characteristic of the crops evaluated based on the SIMPER analysis, *i.e.* these taxa contributed most to within-group similarity (Table 2).

Table 1. Wald statistics generated from linear mixed model repeated measurement analysis for the effect of sampling time and crop on aphid abundance.

	Green bucket (alate adults)			Leaf count (nymphs and apterous adults)			Sweep net (nymphs and apterous adults)		
Effect	Wald statistic	d.f.	*P*	Wald statistic	d.f.	*P*	Wald statistic	d.f.	*P*
Week	31.25	5	<0.001	44.64	5	<0.001	15.00	5	0.013
Crop	40.40	4	<0.001	460.90	4	<0.001	578.70	4	<0.001
Week × crop	48.88	20	<0.001	105.19	20	<0.001	22.65	20	0.323

Table 2. Mean abundance ($\bar{y}_i$) of characteristic (taxa contributing most to within-group similarity) aphid species/species groups in crops. Species are listed in order of their contribution to the similarity within a method and crop with a cut-off of the cumulative per cent contribution at 90 %. Species data to calculate Bray-Curtis similarities were fourth root-transformed ($Y^{0.25}$) to take species with low abundances into account.

Method	Crop	Aphid species/species group	$\bar{y}_i$	Contributing %
Green bucket traps (alate adults)	Lucerne	*Tetraneura fusiformis*	11.00	58.18
		Acyrthosiphon pisum	2.17	13.34
		Acyrthosiphon kondoi	2.00	8.00
		Rhopalosiphum padi	0.67	5.74
		Sitobion spp.	0.50	5.21
	Maize	*Rhopalosiphum padi*	1.83	37.35
		Tetraneura fusiformis	1.33	19.06
		Macrosiphum euphorbiae	1.83	16.63
		Metopolophium dirhodum	0.83	15.01
		Sitobion spp.	0.50	7.97
	Potato	*Tetraneura fusiformis*	14.00	96.34
	Soybean	*Tetraneura fusiformis*	9.00	92.48
	Wheat	*Tetraneura fusiformis*	7.67	69.75
		Rhopalosiphum padi	1.17	18.19
		Sitobion spp.	0.67	12.07
Leaf counts (apterous adults)	Lucerne	*Acyrthosiphon pisum*	2.50	57.37
		Acyrthosiphon kondoi	3.17	31.70
	Maize	*Macrosiphum euphorbiae*	67.67	39.95
		Rhopalosiphum padi	23.83	26.52
		Metopolophium dirhodum	32.00	25.93
	Potato	*Macrosiphum euphorbiae*	10.00	68.81
		Myzus persicae	2.40	31.19
	Wheat	*Metopolophium dirhodum*	10.60	60.26
		Rhopalosiphum padi	2.20	27.69
		Sitobion avenae	2.00	7.51
Sweep net (apterous adults)	Lucerne	*Acyrthosiphon kondoi*	125.50	57.02
		Acyrthosiphon pisum	63.33	40.71
	Maize	*Rhopalosiphum padi*	1.40	73.81
		Macrosiphum euphorbiae	0.80	26.19
	Potato	*Macrosiphum euphorbiae*	3.67	89.61
		Myzus persicae	0.83	7.77
	Wheat	*Rhopalosiphum padi*	2.33	35.95
		Metopolophium dirhodum	3.17	28.74
		Sitobion spp.	4.33	22.60
		Macrosiphum euphorbiae	0.67	9.56

Species that have been reported as vectors of PVY (Ragsdale *et al.* 2001) and that have been recorded in the current study include *A. pisum, Aphis craccivora* Koch, *A. fabae*, *Aphis gossypii* Glover, *Aphis spiraecola* Patch, *Aphis* spp., *Dysaphis* spp., *Hyperomyzus lactucae* (L.), *M. euphorbiae*, *M. dirhodum*, *M. persicae*, *R. maidis*, *Rhopalosiphum nymphae* (L.), *R. padi*, *S. avenae*, *Sitobion fragariae* (Walker), and *Sitobion* spp. With the exception of the characteristic species, they occurred in low numbers only (Table 3).

Only two of the characteristic species recorded, *M. euphorbiae* and *M. persicae*, colonize potato. *Macrosiphum euphorbiae* was a characteristic species recorded landing in green bucket traps in maize. It was the most abundant species colonizing maize

Table 3. Aphid species and abundance recorded on lucerne (Luc), maize (Mz), potato (Pot), soybean (Soy) and wheat (Wht) at the University of Pretoria Experimental Farm from April to May 2006.

Aphid species	Green bucket trap (alate adults)					Leaf counts (apterous adults)					Sweep net (apterous adults)				
	Luc	Mz	Pot	Soy	Wht	Luc	Mz	Pot	Soy	Wht	Luc	Mz	Pot	Soy	Wht
Acyrthosiphon kondoi Shinji	22		1	2	1	19					753	1	1	2	9
Acyrthosiphon pisum (Harris)	24				2	15					380			1	2
Aphis craccivora Koch	1			1											
Aphis fabae Scopoli	1		4	6	3						1				
Aphis gossypii Glover			2												
Aphis nerii Boyer de Fonscolombe	1	1		1											
Aphis spiraecola Patch	1	1		1											
Aphis spp.	1	1		1									2		
Brachycaudus spp.			1												
Dysaphis spp.					1										
Geoica lucifuga (Zehntner)					1										
Hyperomyzus lactucae (L.)			1	2											
Hysteroneura setariae (Thomas)			1												
Macrosiphum euphorbiae (Thomas)	3	20	4	2		15	406	50		4		4	22	2	4
Melanaphis sacchari (Zehntner)															1
Metopolophium dirhodum (Walker)	1	12			6	10	192		1	53	1	2	5	1	19
Micromyzus spp.	1	1		1											
Myzocallis castanicola Baker	2		1	1	1										
Myzus persicae (Sulzer)	4		2		1			12		1			5	1	
Neotoxoptera oliveri (Essig)				1	1										
Paoliella spp.			1												
Rhopalosiphum maidis (Fitch)				1	1										6
Rhopalosiphum nymphae (L.)					1										
Rhopalosiphum padi (L.)	6	12	2	2	7	10	143		2	11	1	7	1	1	14
Rhopalosiphum rufiabdominalis (Sasaki)				1											

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Table 3 (continued)

Aphid species	Green bucket trap (alate adults)					Leaf counts (apterous adults)					Sweep net (apterous adults)				
	Luc	Mz	Pot	Soy	Wht	Luc	Mz	Pot	Soy	Wht	Luc	Mz	Pot	Soy	Wht
Saltusaphis scirpus Theobald	1				1										
Schizaphis spp.			1												
Sitobion avenae (F.)				1			8			10					
Sitobion fragariae (Walker)					1										
Sitobion howlandae (Eastop)							1								
Sitobion spp.	3	3	2	2	5		17			2					26
Tetraneura fusiformis (Sasaki)	73	9	97	57	47										
Therioaphis trifolii (Monell)	2		1	3							11		1		
Uroleuchon sonchi (L.)		1													
Total	**147**	**61**	**121**	**86**	**80**	**69**	**767**	**62**	**3**	**81**	**1147**	**14**	**37**	**8**	**81**

based on leaf count samples. This species was also characteristic for colonizing potato based on leaf count and sweep-net samples, and wheat based on sweep-net samples. *Myzus persicae* was characteristic for colonizing potato. This species together with *M. euphorbiae* contributed 100 % of the within-group similarity based on leaf counts and 97 % based on sweep-netting.

Among species that do not colonize potato, *A. kondoi* and *A. pisum,* which colonize Fabaceae (Millar 1994), were characteristic species landing in green bucket traps in lucerne. The two species were also characteristic taxa that colonized lucerne based on both leaf count and sweep-net sampling methods and together contributed 88 and 98 % to within-group similarities (Table 2). In contrast to sweep-netting, the two species were not recorded from the other four crops with the leaf count method (Table 3).

Of those aphids that colonize Poaceae, *M. dirhodum* was a characteristic species landing in maize and characteristic for colonizing maize and wheat based on leaf count samples and wheat based on sweep-net samples (Table 2). *Rhopalosiphum padi* was a characteristic species landing in green bucket traps in lucerne, maize and wheat plots, although it occurred in relatively low numbers it made the highest contribution to the within-group similarity. This species was characteristic for colonizing maize and wheat based on leaf count and sweep-net samples. Although *Sitobion* spp., many of which colonize Poaceae (Millar 1994), was classified as a characteristic species landing in lucerne, maize, and wheat, contributing between 5 and 12 % to within-group similarity, it was only recorded in low numbers (≤5). This taxon was characteristic for colonizing wheat based on sweep-net samples. In addition, *Sitobion avenae* was recorded as a characteristic species on wheat based on leaf count samples (Table 2). *Tetraneura fusiformis*, a root-feeding aphid (Blackman & Eastop 2006), was the dominant species landing in green bucket traps in lucerne, potato, soybean, and wheat plots, contributing between 58 and 96 % to within-group similarities. This species was also characteristic for maize, contributing 19 % to within-group similarity. *Tetraneura fusiformis* was the only characteristic species landing in potato and soybean.

The proportion of aphids recorded using leaf count and sweep-net sampling differed depending on aphid and plant species (Table 3). For example, a higher number of adult apterae of *A. kondoi* and *A. pisum* were recorded on lucerne based on sweep net sampling (753 and 380 individuals) compared with leaf counts (19 and 15 individuals), whereas for *M. euphorbiae* leaf counts on maize were higher (406 individuals) compared to sweep samples (four individuals).

DISCUSSION

The most abundant potato-colonizing species collected during the current study were *M. euphorbiae* and *M. persicae*, and the most abundant non-colonizing species *A. kondoi*, *A. pisum*, *M. dirhodum*, *R. padi*, *Sitobion* spp., and *T. fusiformis*. With the exception of *A. kondoi* and *T. fusiformis*, whose PVY vector status is unknown, these species have been reported to be vectors of PVY (Ragsdale *et al.* 2001).

Landing patterns of aphids in the current study suggest that alate adults of some of the species recorded may have the ability to discriminate between host plants in the pre-alighting phase, landing more frequently on the crops they colonize. *Acyrthosiphon kondoi* and *A. pisum*, which colonize Fabaceae, showed a preference for landing in green bucket traps in lucerne, a crop that they also colonized. *Metopolophium dirhodum*, which colonizes Poaceae, landed most frequently in green bucket traps in maize and was characteristic for colonizing maize and wheat. These findings suggest that these species may have the ability to locate the preferred host plant, if present, within a habitat patch prior to landing.

This is in accordance with previous work that visual as well as olfactory cues from host plants may affect host plant choice of some aphid species prior to landing. For example, *Cavariella aegopodii* (Scopoli), an aphid species that colonizes Apiaceae (Umbelliferae), was attracted in the field to the volatile carvone, which amongst others occurs in some Apiaceae (Chapman *et al.* 1981). In addition, differences in spectral reflectance between leaves of different plants may influence the landing response of alates (Döring & Chittka 2007). The host choice of populations of a given species may be highly specialized, although a range of host plant species may be available (Bernays & Funk 1999). According to Caillaud (1999), specialized populations of *A. pisum*, which were adapted to either clover or lucerne (alfalfa), did not distinguish between the two plant species in the pre-landing phase. In contrast, *Myzus persicae*, a polyphagous species that has been recorded on plant species belonging to more than 40 families (Millar 1994), was able to locate its host plant in the pre-alighting phase, depending on the host form (Margaritopoulos *et al.* 2005), as an olfactory complimented by a visual response (Vargas *et al.* 2005). The work of Chapman *et al.* (1981) and Caillaud (1999) suggests that cues common to a range of host plants may be used in the pre-alighting phase.

Not all species distinguished between host and non-host plants prior to landing. Of the cereal aphids in the current study, *R. padi* and *T. fusiformis* appeared to be less discriminating when landing in a crop than *M. dirhodum*. *Rhopalosiphum padi* not only landed relatively frequently in green bucket traps in maize and wheat, which it colonized, but also in the non-host lucerne. This is in agreement with Åhman *et al.* (1985), who observed that spring and summer migrants of *R. padi* did not distinguish between hosts and non-hosts in the pre-alighting phase. Similarly, *T. fusiformis*, a common species in the current study that has been recorded to colonize several grasses including rice and sorghum in Africa (Millar 1994), landed frequently in green bucket traps in all crops evaluated in the current study. The results for *R. padi* and *T. fusiformis* support findings that some aphid species seem to discriminate between host and non-host plants only after landing on a plant (Kennedy *et al*. 1959; Powell & Hardie 2000; Powell *et al.* 2006). Too few alate adults of *Sitobion* spp. that tended to colonize wheat in the current study were collected to determine landing preference.

A crop border should be preferred by aphids to the main crop (Nault *et al.* 2004). The current study evaluated aphid landing preference and plant colonization to identify plants species that promote aphid settling to decrease vector activity in seed potato fields.

Of the PVY vector species recorded, only two, *M. euphorbiae* and *M. persicae*, were characteristic for colonizing potato in the current study. *Macrosiphum euphorbiae*, a polyphagous species that utilizes plant species from more than 20 families (Millar 1994), colonized both maize and potato but preferred to land in maize plots. *Myzus persicae* colonized potato. Landing preferences of this species could not be determined because numbers recorded were too low.

DiFonzo *et al.* (1996) showed that soybean as a crop border for potato reduced PVY infection of potato plants. Although aphids did land in green bucket traps in soybean in the present study, colonization of this crop by aphids was very low. This could be due to the high trichome density of soybean leaves, which reduces probing (Gunasinghe *et al.* 1988) and increases the likelihood of aphids re-alighting and spreading PVY to seed potatoes. This crop may not be a suitable border plant in South Africa because cultivars planted in this country usually have a high trichome density (W. van Wyk, pers. comm.).

When selecting a crop border plant it is important to consider plant diseases that the crop border plant may have in common with potatoes and which could be transmitted from the crop border to potatoes. Lucerne as a crop border plant may therefore not be viable in regions where Alfalfa mosaic virus (AMV; Lucerne mosaic virus), a non-persistently aphid-transmitted virus infecting both lucerne and potatoes (Mughal *et al.* 2003) is present. Of the many aphid species able to transmit AMV (Garran & Gibbs 1982; Paliwal 1982; Mughal *et al.* 2003), several were recorded in the present study (*A. pisum, A. kondoi, A. gossypii, Therioaphis trifolii* (Monell), and *M. persicae*). However, lucerne is planted in some seed potato growing regions in South Africa and could serve as a border crop where *A. pisum*, which preferred to land in and colonized lucerne in the current study, is an important vector of PVY.

Oats, sorghum, and wheat were tested as crop border plants and found to be effective in reducing PVY incidence (DiFonzo *et al.* 1996; Thieme *et al.* 1998). Significantly more aphids landed in green bucket traps in potato compared to maize and wheat in the current study. This is due to *T. fusiformis*, which made up 96 % of all aphids recorded in green bucket traps in potato. Based on species composition of all three sampling methods combined, maize and wheat were preferred to potato and lucerne by, for example, *M. euphorbiae*, *M. dirhodum* and *R. padi*; all three species colonize Poaceae (Millar 1994). Thus, in regions where cereal aphids characterize aphid populations, maize and wheat could be suitable border crops. For example, Thieme *et al.* (1998) found aphid species occurring in potato fields to be mainly cereal aphids, which can be important vectors of PVY (Harrington *et al.* 1986; Harrington & Gibson 1989; de Bokx & Piron 1990; Ragsdale *et al.* 2001). In South Africa, *R. padi* is a dominant species in potato fields in some regions (K. Krüger, pers. obs.). In addition, maize could act as a physical barrier intercepting migrant aphids (Damicone *et al.* 2007), depending on the virus spread pattern (monocyclic or polycyclic) and the height of the barrier crop when aphid vector pressure is highest (Fereres 2000). In the present study, alate aphid species characteristic of the plots surrounding maize differed from those characteristic of maize, indicating that the maize did not have a barrier effect.

The findings of the current study on aphid landing preferences raise questions on how aphids relate to host plant-specific cues during the pre-alighting phase. Therefore, future studies should determine and compare the attractiveness of specific host plant cues to obtain a better understanding of the mechanisms involved in host plant selection in this phase to aid in the development of management strategies to reduce PVY transmission in seed potatoes, such as crop borders.

In conclusion, the combined results on aphid landing and colonization of the crops evaluated indicate that maize and wheat have potential as crop border plants in regions where aphids colonizing Poaceae, and lucerne in regions where aphids colonizing Fabaceae are abundant. Soybean cultivars with high trichome density, which reduce aphid colonization, are less suitable. The current study served to identify potentially suitable crop border plant species. Crop border trials will have to be carried out in the respective South African seed potato-growing regions during seed potato growth periods for further evaluation.

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