

RESEARCH

Landing Preference and Reproduction of *Rhopalosiphum padi* (Hemiptera: Aphididae) in the Laboratory on Three Maize, Potato, and Wheat Cultivars

Michelle L. Schröder,¹ Robert Glinwood,² Rickard Ignell,³ and Kerstin Krüger^{1,4}

¹Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Pretoria, 0028, South Africa

²Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

³Unit of Chemical Ecology, Department of Plant Protection Biology, Swedish University of Agricultural Sciences, Alnarp, Sweden

⁴Corresponding author, e-mail: kkruger@zoology.up.ac.za

Subject Editor: Phyllis Weintraub

J. Insect Sci. (2015) 15(1): 63; DOI: 10.1093/jisesa/iev048

ABSTRACT. The bird cherry—oat aphid *Rhopalosiphum padi* (L.) transmits the nonpersistent *Potato virus Y* (PVY) to seed potatoes. Planting a nonvirus host plant around the main crop can reduce PVY incidence, because aphids tend to land in high numbers at the edge of a field and the crop border acts as a virus sink. This study determined *R. padi* landing and settling preferences and reproductive rates on three cultivars each of maize and wheat compared with potato in the laboratory as a basis for identifying an attractive crop border plant. Aphids were reared on maize and wheat to control for bias due to previous experience. Irrespective of origin, alates preferred to land almost exclusively on maize and wheat rather than on potato cultivars in choice experiments. Aphid settling on the maize and wheat cultivars depended on aphid origin. In no-choice experiments, *R. padi* produced the highest number of offspring on the wheat cultivars, irrespective of origin. Plant nitrogen content and trichome density did not influence *R. padi* reproduction. The study demonstrates that host plant preference of aphids may vary between plant cultivars and can therefore influence the effectiveness of a crop border. The high landing rate but low reproduction suggest that maize cultivars ‘6Q-121’ and ‘78-15B’ could be suitable crop border plants in regions where *R. padi* is abundant. Before testing potential crop border plants in the field, cultivars should be screened using aphid landing, settling and reproduction as selection criteria.

Key Words: bird cherry—oat aphid, host plant selection, crop border plants, *Potato virus Y*, trap crops

Potato virus Y (PVY) causes major economic losses in the seed potato industry world-wide (Radcliffe and Ragsdale 2002). PVY is mainly transmitted in a nonpersistent manner by aphid (Hemiptera: Aphididae) vectors. Although wingless aphids (apterae) are able to transmit viruses, it is the winged (alate) aphids, when probing a potential host plant, that are mainly responsible for spreading viruses in crops over long distances (Bradley 1954; Powell 1991; Radcliffe and Ragsdale 2002). Current preventative measures include the use of seed with low PVY infection, reduction of virus inoculum and the use of crop borders to reduce the number of aphid vectors landing in potato fields and to decrease virus incidence (Radcliffe and Ragsdale 2002; Hooks and Fereres 2006). These preventative measures, especially crop borders, rely on a good understanding of the host plant searching behavior of the most abundant aphid vector species.

During their initial prealighting behavior, aphids use visual cues to orientate toward potential host plants, and plant chemical cues to discriminate between host and nonhost plants (Kennedy et al. 1961; Pickett et al. 1992; Powell et al. 2006). After landing on a plant, a variety of surface characteristics, such as trichome exudates, epicuticular waxes and topology further influence the aphids’ choice (Powell et al. 2006). The decision to accept or reject a plant is not only based on plant characteristics; the plant on which the aphid developed may also play a role (Guldmond 1990; Barron 2001; Gorur et al. 2007). Aphid populations only produce alates after several generations of apterae when the colony is larger than the plant can sustain (Müller et al. 2001). This could cause aphids to become adapted to the plant species they originated from, and they may therefore prefer to reproduce on the same plant species rather than on other species within their host range (Barron 2001; Gorur et al. 2007).

PVY is best controlled by cultural management strategies (Radcliffe and Ragsdale 2002). Crop borders rely on the response of aphids to the contrast in wavelength reflectance between the brown–green interface

at the edge of the crop (Minks and Harrewijn 1988). Replacing the edge with a nonvirus host plant creates a virus sink (DiFonzo et al. 1996; Hooks and Fereres 2006). For example, DiFonzo et al. (1996) reported a reduction in PVY incidence in potato fields planted with a crop border of sorghum (*Sorghum bicolor* L., Poaceae), wheat (*Triticum aestivum* L., Poaceae), and soybean (*Glycine max* L., Fabaceae). However, they found no reduction in the number of aphids landing in the fields with crop borders. Nault et al. (2004) suggested that using trap crops (crop species more attractive to the insect pest than the primary crop) may in some crops increase the number of aphids landing in the crop border in comparison to the main crop. For example, Toba et al. (1977) found a reduction in the incidence of *Watermelon mosaic virus* (WMV-1 and -2) when musk melon (*Cucumis melo* L., Cucurbitaceae) was planted with a crop border of wheat. However, trap crops may serve as a host for vector reproduction and thus increase virus spread in nearby crops (Hooks and Fereres 2006). Hence, control methods such as crop borders to reduce the incidence of nonpersistent viruses rely on understanding the relationship between the main vector species and host plant for each crop.

Rhopalosiphum padi (L.) (Hemiptera: Aphididae) is an important vector of PVY (Sigvald 1987; Radcliffe and Ragsdale 2002). This aphid species does not colonize potato (*Solanum tuberosum* L., Solanaceae) but transmits PVY to seed potato fields when searching for good quality host plants (Boiteau 1997). Although *R. padi* is a less efficient vector than potato-colonizing species such as *Myzus persicae* (Sulzer), high numbers of *R. padi* in seed potato fields can result in high infection rates (Van Hoof 1977; Sigvald 1987). In addition, early season flights of *R. padi* can advance PVY infection (Van Hoof 1977).

Maize (*Zea mays* L., Poaceae) and wheat have been identified as potential crop border plants, when compared with lucerne (*Medicago sativa* L., Fabaceae) and soybean in seed potato-producing regions where *R. padi* is abundant (Schröder and Krüger 2014). Although more aphids

landed on maize and wheat than potato, the relative attractiveness of *R. padi* to different maize and wheat cultivars was not considered (Schroder and Kruger 2014). It is known that aphid preference may vary between plant cultivars of the same species (Storer et al. 1993; Storer and van Emden 1995; Alla et al. 2003), and using a more attractive cultivar that supports a low population density may increase the number of aphids landing in the border crop without becoming a source of aphid vectors. Therefore, the relative attractiveness of different crop cultivars compared with the main crop needs to be considered when evaluating potential trap crops to be used as crop border plants. This study evaluated the landing and settling preferences, and reproduction of *R. padi* on three cultivars each of maize, potato, and wheat in a laboratory study as a basis for identifying wheat and maize varieties with the best combination of attractiveness to *R. padi* and low population density.

Materials and Methods

Plants. Three cultivars each of maize (cultivars ‘CRN 3505’, ‘6Q-121’, and ‘78-15B’), wheat (cultivars ‘Duzi’, ‘Karioga’, and ‘Krokodil’), and potato (cultivars ‘BP1’, ‘Hertha’, and ‘Mondial’) were used in the experiments. Three potato cultivars were included to control for possible effects on *R. padi* landing behavior due to cultivar differences. Plants were grown in an autoclaved soil mixture consisting of river sand and coco peat in a ratio of 4:1 in 12.5-cm-diameter pots. Three maize seeds and two rows of wheat seeds, each row containing 10 seeds, of the same cultivar were sown into pots. The seeds were treated with fungicides. In addition, two presprouted potato mini tubers of the same cultivar were planted per pot. The number of seeds and tubers was chosen to ensure that all plants had a comparable leaf area when used in the experiments. No pesticides were applied to the plants during the study. Agricultural lime (5 ml per pot) and slow release fertilizer [c. 1.6 g per pot; Grovida, Khula Kahle Fruit and Flower, N:P:K (3:1:5)] were added to the soil upon planting. Two weeks after planting, a weekly foliage treatment of micronutrients (Trelmix trace element solution) was applied to the plants according to the manufacturer’s instructions. The plants were grown in a climate controlled room at 25°C, ambient relative humidity (RH), and a photoperiod of 16:8 (L:D) h. The maize and wheat plants were used in experiments at growth stages 11 and 12 with two to three leaves unfolded, and the potato plants at growth stages 17 and 18 with seven and eight leaves unfolded (Meier 2001). The leaf area was determined with a leaf area meter (Li-3100C, Li-Cor, Lincoln, Nebraska, USA).

Insects. A culture of *R. padi* was established at the University of Pretoria in 2009 with aphids obtained from a culture maintained on wheat at the Agricultural Research Council—Small Grain Institute (ARC—SGI) in Bethlehem, South Africa. The aphids were originally collected from wheat plants at the Tygerhoek experimental farm, Riviersonderend, Western Cape (34° 9' S, 19° 54' E), and supplemented with individuals collected from wheat. Aphids were reared in ventilated wooden cages with a glass panel at the top (45 × 55 × 32 cm) in a climate-controlled room at 22°C, ambient RH, and a photoperiod of 16:8 (L:D) h. The insects were reared either on mixed cultivars of maize or on mixed cultivars of wheat. Aphids were reared on respective host plants for more than 6 months before use in experiments. *R. padi* takes 6 and 22 d to complete a generation at 13 and 26°C, respectively (Villanueva and Strong 1964). Therefore, several generations of *R. padi* were produced on the respective host plants before being used in experiments and were thus adapted to both host plant and experimental conditions.

Alate virginoparae were produced by crowding the aphids on plants. Only actively moving/walking alates of various ages were collected with a paint brush from the top glass panel of the cages and carefully placed into a glass vial with a gauze covered opening in the lid. To control for possible effects of previous experience, separate experiments were carried out with aphids reared on maize and wheat.

Landing and Settling Preference, and Reproduction—Choice Experiment. For aphids reared on wheat, five rows of plants were placed in a randomized block design in a light gray-walled climate-controlled room with a gray cement floor. Each row contained nine pots, each with one of the plant cultivars, placed 40 cm apart. Alatae aphids were released by placing glass vials containing the aphids with their lids removed on release podiums (height: 30 cm). In total, 115 alate aphids reared on wheat were released evenly within the five rows of plants for each replicate. The aphids were released in groups of 10 aphids for every four plants, except for the uneven rows where five aphids were released between groups of two plants, at plant canopy height to ensure that each plant had an equal chance of aphids landing and colonizing. The experiment was carried out at 24.1 ± 0.1°C, 50.6 ± 2.7% RH, and a photoperiod of 16:8 (L:D) h (cool white fluorescent lights; Osram, Indonesia). The experiment was repeated five times.

Aphids reared on maize produced a considerably lower number of alates than those reared on wheat, and the experimental design was adjusted accordingly. Pots with plants were arranged in a circle consisting of one pot of each plant cultivar placed randomly. Twenty-three alate aphids reared on maize were released in the center of the plant circle at plant canopy height. The experiment was carried out in a climate-controlled room under the conditions described earlier, except that a gauze cage (80 × 80 × 30 cm) was placed over the plants on the floor. The experiment was repeated five times.

For both aphids reared on wheat and on maize, alates were counted on the plants 4 h (landing) and 24 h (settling) postrelease. The time that alate *R. padi* took to land on plants after being released was determined in a pilot study in which the aphids were observed until they landed on plants. Aphids were left to reproduce for 14 d, after which the number of nymphs and apterous adults produced on each plant was counted.

Aphid Reproduction—No-Choice Experiment. The three maize and wheat cultivars were randomly arranged in six rows in a greenhouse, with each row containing one of each crop cultivar. A modified ventilated 2 liters plastic bottle was placed over the plants in each pot to contain the aphids. Potato was excluded because it is not a host plant for *R. padi* and no offspring were recorded in the choice experiment. Five actively moving adults were collected in small glass vials, and the vials were placed on the soil in each pot where the aphids were allowed to move freely onto the plants. The study was undertaken separately with alatae from maize and from wheat, as well as apterae from maize and from wheat. The greenhouse temperature was 20.5 ± 0.6°C, 43.1 ± 1.5% RH at midday, with average maximum and minimum temperatures of 24.8 ± 0.6°C and 10.3 ± 0.5°C, a maximum and minimum of 71.9 ± 1.5% and 26.8 ± 1.5% RH, and with natural light conditions from May to August 2012. The number of aphids was counted at 24-h intervals for 14 consecutive days. The experiment was replicated five times.

Nitrogen Analysis. To determine the nitrogen content of maize and wheat cultivars, leaves of a subset of plants were weighed and dried in an oven at 55°C for 48 h. The dried plant material was weighed using a Mettler Toledo PB303-L (Mettler-Toledo AG, Laboratory & Weighing Technologies, Greifensee, Switzerland) scale and ground into a fine powder with a Tecator sample mill (Cyclotec 1093, Foss Tecator AB, Höganäs, Sweden). To obtain enough material for the analysis, leaves from five plants were pooled to form a replicate. Five replicate samples of each cultivar were submitted for nitrogen analysis. The nitrogen content of the plants was determined at the UP Nutrilab, Department of Animal Science, University of Pretoria, with the Dumas method (AOAC 2000). Potato was excluded from the nitrogen analysis because *R. padi* did not settle or reproduce on potato during the choice trial.

Trichome Density. To determine leaf trichome density, 1-cm-long sections were cut from the leaf blades across the width of maize and wheat leaves. The trichome density of potato leaves was not determined because *R. padi* did not settle or reproduce on potato during the choice trial. The leaf sections were cleared in a 1:1 (v:v) mixture of phenol and chloral hydrate for 24 h. Leaf sections were transferred to lactic acid

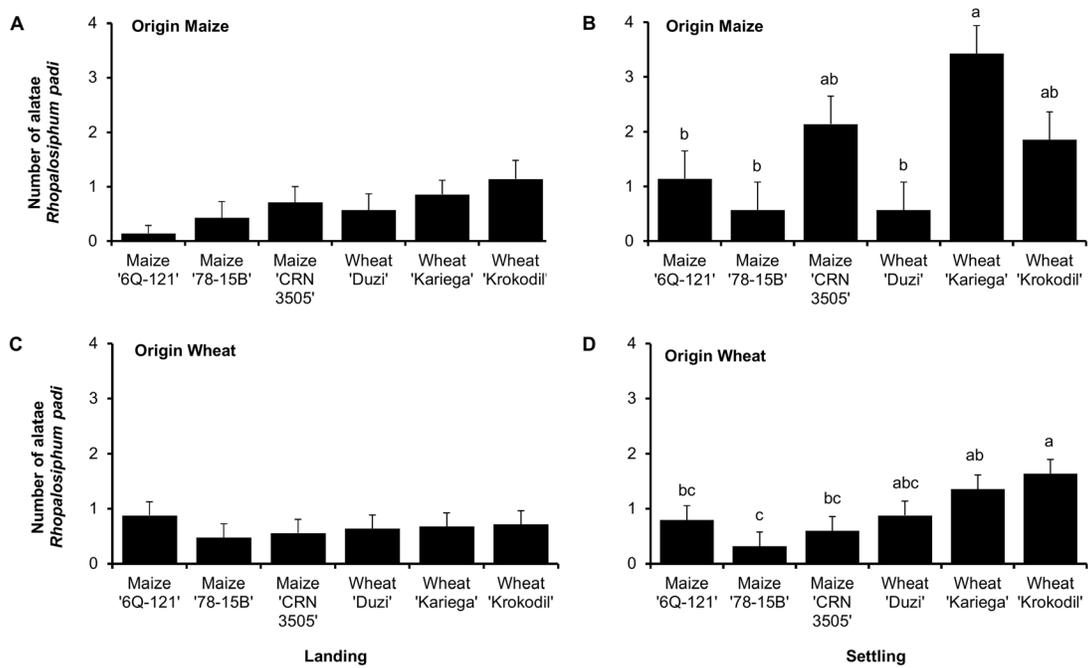


Fig. 1. *Rhopalosiphum padi* (mean \pm SE) landing (A, C) and settling (B, D) on three maize and three wheat cultivars. Aphids were reared on maize (A, B) or wheat (C, D). Letters above bars indicate significant differences between means (LSD test: $P < 0.05$).

and mounted on microscope slides (Hoxie et al. 1975). Photographs of the trichomes were taken using a Nikon Optihot microscope and a Nikon digital camera (DXM 1200F) (Nikon Instruments, Tokyo, Japan) at $40\times$ magnification. All trichomes on the abaxial side of the leaf surface along the midvein as well as the leaf midsection were counted in 1×1 mm squares. Aphids feed on the abaxial side of leaves, therefore the adaxial leaf surfaces was excluded.

Statistical Analyses. The numbers of landing and settling aphids, as well as the number of offspring produced on the three maize, potato, and wheat cultivars in the choice experiment with *R. padi* reared on maize were analyzed with a one-way analysis of variance (ANOVA). The data on *R. padi* reared on wheat were analyzed with a nested ANOVA with cultivar as factor and landing, settling, and reproduction as variates. Fisher's least significant difference (LSD) test was used to separate means. Potato was excluded from all analyses because only one aphid landed on one of the cultivars, and none settled or reproduced on potato. For the no-choice experiment, linear mixed model repeated measurement analysis was used to determine differences in aphid counts on maize and wheat cultivars over 14 d. The counts were transformed by $\log_e(x + 0.5)$ to normalize data and stabilize treatment variances. Fixed factors were aphid origin, plant cultivar and aphid origin \times cultivar interaction, and cage \times day was entered as random factor. Fisher's LSD test was used to separate means. Data were analyzed with GenStat (Payne et al. 2012).

Leaf areas were analyzed with a Kruskal–Wallis ANOVA followed by multiple comparisons of mean ranks for all groups. Separate ANOVAs were used to determine significant differences in plant nitrogen content, as well as in trichome density among plant cultivars. Fisher's LSD test was used to distinguish between means. Statistica (Version 11 Statsoft, Inc. 1984–2012) was used for the data analyses.

The significance level was set at $P < 0.05$ for all analyses.

Results

Landing and Settling Preferences, and Reproduction—Choice Experiment. There was no significant difference in the leaf area among the plant species and cultivars used ($H = 13.1$, $df = 8$, $P = 0.11$); leaf area ranged between 78 and 127 cm^2 .

For *R. padi* reared on maize, the number of alates landing did not differ significantly between the maize and wheat cultivars ($F_{5,41} = 1.73$, $P = 0.16$; Fig. 1a). However, the number of alates settling on wheat 'Kariega' was approximately three times higher than that settling on maize '6Q-121' and six times higher than alates settling on maize '78-15B' and wheat 'Duzi' ($F_{5,41} = 2.97$, $P = 0.03$; Fig. 1b). No significant differences were observed in the number of adult apterae and nymphs produced after 14 d ($F_{5,41} = 1.34$, $P = 0.274$; Fig. 2a).

For *R. padi* reared on wheat, a similar number of alatae landed on the three maize and wheat cultivars ($F_{5,149} = 0.49$, $P = 0.785$; Fig. 1c). However, the number of alate aphids that settled on wheat 'Krokodil' was more than twice that settling on the three maize cultivars ($F_{5,149} = 3.22$, $P = 0.009$; Fig. 1d). After 14 d the number of *R. padi* nymphs and adult apterae was significantly higher on wheat 'Kariega' than on any other maize or wheat cultivar, and higher on wheat 'Duzi' and 'Krokodil' compared with the maize cultivars ($F_{5,149} = 19.80$, $P < 0.001$; Fig. 2b).

Aphid Reproduction—No-Choice Experiment. Reproduction of *R. padi* on the three different maize and wheat cultivars was significantly influenced by plant cultivar, and also by the origin of the aphids (morph and plant species). Significant interactions were observed between the number of days and origin, and between origin and plant cultivar ($P < 0.05$; Table 1).

Over the 14-d trial period, significantly higher numbers of *R. padi* were recorded on the three wheat cultivars in comparison to the three maize cultivars (Fig. 3). The origin of *R. padi* had a significant effect on the number of adults and nymphs counted over 14 d, with the highest number produced from apterae reared on wheat, followed by alatae reared on maize and wheat and apterae reared on maize (Table 1; Fig. 3).

R. padi alatae reared on maize and wheat produced a significantly higher number of offspring on the three wheat cultivars compared with the three maize cultivars (Fig. 3a and b). Likewise, the number of offspring produced by *R. padi* apterae originating from both maize and wheat was significantly higher on the three wheat cultivars compared with the three maize cultivars (Fig. 3c and d). In addition, for *R. padi* apterae originating from maize, the number of offspring produced was significantly lower on maize '6Q-121' than maize '78-15B' (Table 1; Fig. 3c).

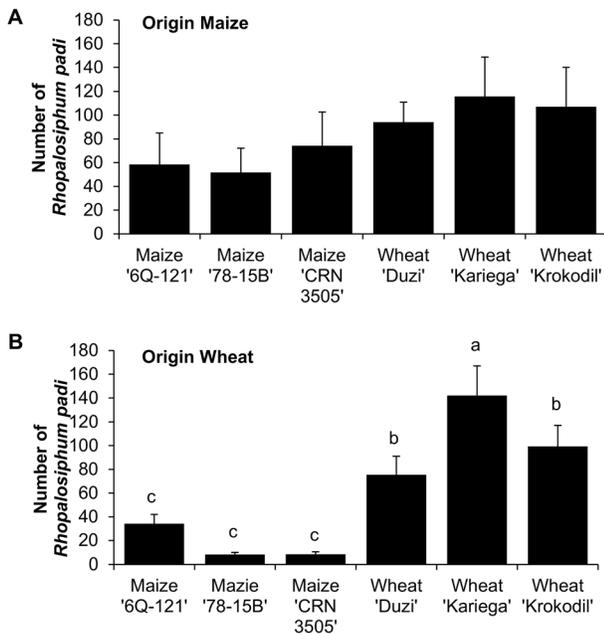


Fig. 2. Increase in number of *R. padi* (mean ± SE) after 14 d on three maize, and three wheat cultivars. Aphids were reared on maize (A) or wheat (B). Letters above bars indicate significant differences between means (LSD test: $P < 0.05$).

Nitrogen Analysis. No significant differences were found in leaf nitrogen content of the three maize and wheat cultivars ($F_{5,24} = 1.77$, $P = 0.16$; Table 2).

Trichome Density. No trichomes were found on the leaves of the three maize cultivars. However, intraspecific differences in trichome density were found in wheat cultivars for both the midvein ($F_{2,27} = 8.8$, $P < 0.01$; Table 2) and the middle section of the leaf ($F_{2,26} = 11.83$, $P < 0.01$; Table 2). Along the midvein of the leaves, trichome density of wheat 'Krokodil' was significantly lower than in the wheat cultivars 'Kariega' and 'Duzi'. In the middle section of the leaves between the midvein and the edge of the leaf blade, wheat 'Duzi' had the highest trichome density, followed by the wheat cultivars 'Kariega' and 'Krokodil'.

Discussion

Developing nonpersistent virus control strategies, such as the use of crop border plants, relies on an understanding of interactions between the insect vector and crop plant. In this study, we show that *R. padi* landed in similar numbers on maize and wheat cultivars, regardless of the plant species they originated from, whereas only one individual landed on the potato cultivars. Moreover, *R. padi* showed intraspecific differences in settling and reproduction rates between the maize and wheat cultivars, depending on the plant species they originated from. This suggests that alate *R. padi* use plant cues to orientate toward their host but will only make a final choice among host plants after plant contact and initial probing has taken place. In a field study on aphid plant preference, a higher number of *R. padi* landed in maize, wheat and lucerne (nonhost plant) than in potato plots, but colonized (settled and reproduced) maize and wheat (Schröder and Krüger 2014). Taken together, the results of the cited field study and the current laboratory study suggest that maize and wheat are suitable crop border plants for potato.

After plant contact and gustatory evaluation, arrestment or take-off occurs depending on the plant characteristics perceived by the aphids (Bruce et al. 2005; Powell et al. 2006). In this study, *R. padi* alatae landed in similar numbers on maize and wheat cultivars but subsequently settled in significantly different numbers on these cultivars.

Table 1. Test statistics generated from the linear mixed model repeated measurement analysis of the number of *Rhopalosiphum padi* offspring recorded over 14 d on maize 'CRN 3505', '78-15B', '6Q-121' and wheat 'Duzi', 'Kariega', and 'Krokodil'

Fixed term	Wald statistic	n.d.f.	F statistic	P-value
Days	1.93	13	0.15	1.00
Origin	1,160.54	3	386.85	<0.001
Cultivar	112.82	5	22.56	<0.001
Days × origin	57	39	1.46	0.034
Days × cultivar	26.26	65	0.40	1.00
Origin × cultivar	271.52	15	18.10	<0.001
Days × origin × cultivar	102.7	195	0.53	1.00

R. padi was reared on maize and wheat.

Table 2. Nitrogen content of three maize and wheat cultivars and trichome density of three wheat cultivars (mean ± SE)

Crop	Cultivar	Nitrogen content (g/100 g dry mass)	Trichome density (count per mm ²)	
			Midleaf abaxial surface	Midvein abaxial surface
Maize	'6Q-121'	4.41 ± 0.34	–	–
	'CRN 3505'	4.66 ± 0.22	–	–
	'78-15B'	4.82 ± 0.24	–	–
Wheat	'Duzi'	5.18 ± 0.27	48.4 ± 8.18 ^a	47.3 ± 6.99 ^a
	'Kariega'	5.05 ± 0.34	31.9 ± 1.36 ^b	46.11 ± 1.92 ^a
	'Krokodil'	5.41 ± 0.21	17.3 ± 3.61 ^b	17.6 ± 4.02 ^b

Letters within columns indicate significant differences (LSD test: $P < 0.05$).

More individuals settled on wheat 'Kariega' than maize '6Q-121', '78-15B' and wheat 'Duzi' when reared on maize. Aphids reared on wheat settled in higher numbers on wheat 'Krokodil' than maize cultivars. The difference in the number of aphids settling between the three maize cultivars and wheat 'Duzi' was not significant, supporting previous findings that settling is influenced by further evaluation of plant surface characteristics and gustatory cues perceived during initial probing behavior (Kennedy et al. 1959; Orlob 1961; Powell 1991). The change in aphid behavior between dispersal flight and landing or settling on a plant is gradual, so that an aphid may take several short flights before being behaviorally ready to settle (Kennedy et al. 1961; Kennedy and Booth 1963). This repeated alighting and taking-off favors the spread of nonpersistent viruses, such as PVY (Kennedy et al. 1959; Kennedy and Booth 1963; Swenson 1968). Once the aphid has landed it probes the plant during the plant contact evaluation phase, which is sufficient for aphids to lose the ability to transmit the virus, and is therefore unlikely to contribute to virus spread when taking-off from the crop border plant (Powell 1991; Powell et al. 1992; DiFonzo et al. 1996). Therefore, planting a crop border plant that is attractive to alate aphids and that is a nonvirus host combines two mechanisms of crop borders; trap crop and virus sink (Hooks and Fereres 2006). Strengthening the edge effect by attracting aphids to the border crop away from the main crop has the potential to reduce aphid activity and in turn reduce the risk of PVY incidence in potato fields.

Using trap crops as border crops may cause pest populations to increase and become a source of alate aphids (Hokkanen 1991; Müller et al. 2001). It is therefore important to select a plant on which aphid population increase is low. From among the maize and wheat cultivars combined, *R. padi* reared on wheat plants settled most frequently on wheat 'Krokodil' and reproduced most successfully on the wheat cultivars evaluated. Aphids reared on maize, on the other hand, settled most frequently on wheat 'Kariega', in comparison to maize '6Q-121', '78-15B' and wheat 'Duzi'. However, no difference was found in the number of offspring produced between the maize and wheat cultivars.

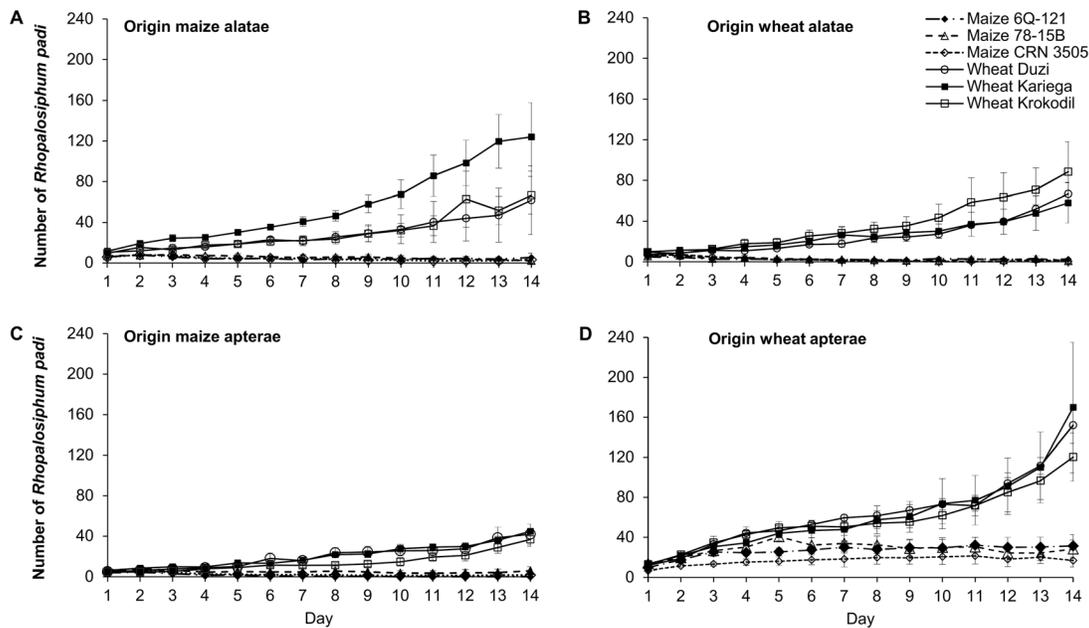


Fig. 3. Number of *R. padi* offspring (mean \pm SE) from alatae reared on maize (A) or wheat (B) and apterae reared on maize (C) or wheat (D) recorded daily over 14 d on three maize and three wheat cultivars.

The higher number of offspring produced on wheat cultivars by aphids reared on wheat could have been due to the higher number of aphids settling on the wheat cultivars rather than wheat being a more suitable host plant. However, in the no-choice trial, the number of offspring produced was higher on wheat than maize for *R. padi* reared on either maize or wheat. Several studies have reported that *R. padi* prefers barley or rye to wheat, as these cereals are more suitable for reproduction (Leather and Dixon 1982; Farrell and Stufkens 1989). However, these studies did not include maize. The results of the present study indicate that wheat may be a more suitable host for *R. padi* than maize. However, this could be due to the aphid population being better adapted to wheat than maize.

The feeding and oviposition preferences of an insect can be modified by a host plant that it has been previously exposed to (Guldemand 1990; Barron 2001), and Gorur et al. (2007). This had a discernible effect on settling and reproductive behavior of *R. padi*. Aphids reared on wheat reproduced higher numbers on wheat in both choice and no-choice experiments. No difference in the number of aphids produced between maize and wheat was found for aphids reared on maize in the choice experiments. Similar observations were made for *Aphis fabae* reared on nasturtium (*Tropaeolum majus* L., Tropaeolaceae) and broad bean (*Vicia faba* L., Fabaceae), where a strong conditioning effect was found for nasturtium but not for broad bean (Gorur et al. 2007). The mechanisms involved in the conditioning effect in aphids is not clear but could be the result of an inheritance of feeding preferences, based on either a genetic effect or due to environmental factors such as cues transmitted by the parental host plant (Guldemand 1990; Barron 2001). Our findings suggest that wheat has a stronger conditioning effect than maize.

Both wheat and maize are used as rotational crops (crops planted in the same field after a potato planting to avoid accumulation of pathogens in the soil) in producing seed potatoes, and *R. padi* may therefore originate from both crops as well as grasses. However, wheat is a winter crop and maize a summer crop in South Africa. Maize would thus be better suited as a crop border plant on which aphid populations do not rapidly reach high levels. However, wheat may be used in regions where potatoes are planted during the winter months.

Plant characteristics such as nitrogen content and trichomes have been found to influence aphid reproduction and population density

(Roberts and Foster 1983; Bethke et al. 1998; Ponder et al. 2001). It is unlikely that plant nitrogen content contributed to the observed differences in reproduction in our study because no differences were found in the nitrogen content of the plants tested. Differences in trichome density were found between the wheat cultivars, but no relationship was found between trichome density and reproduction of *R. padi*. In the choice trials, the higher trichome density in wheat 'Duzi' may have contributed to the lower number of *R. padi* produced in comparison to wheat 'Kariega'. However, no difference was observed in the number of *R. padi* produced on the three wheat cultivars in the no-choice trials. Roberts and Foster (1983) observed a negative relationship between trichome density and aphid numbers in the wheat cultivars studied. It is unlikely that plants with a high trichome density will be good crop border plants because aphids may not transmit the virus before leaving the plant. That said, the maize cultivars did not have any trichomes and the reproduction rate of *R. padi* in the present study was generally lower on the maize cultivars than the wheat cultivars, indicating that other factors may also be involved.

In summary, *R. padi* preferred to land on maize and wheat cultivars compared with potato. Wheat 'Kariega' and 'Krokodil' may be more suitable as crop border plants than the three maize cultivars based on aphid settling rates. However, the three wheat cultivars may be inferior because they supported higher aphid numbers than maize. An accumulation of aphids on the border crop will result in high aphid populations, heightening the risk of virus transmission due to increased aphid activity. Therefore, the maize cultivars may be more suitable as crop border plants in potato-producing regions where *R. padi* is abundant. Consequently, it may be necessary to adapt the strategy for different regions by selecting an attractive border plant suitable for the major vector aphid species in the region.

The study contributes to the development of selection criteria for crop border plants. A crop border plant should be more attractive to the main aphid vectors in a potato growing region than the main crop and support a relatively low aphid population. In addition, plant characteristics such as trichome density can aid in selecting potential crop border plants. Before testing a plant in the field, such characteristics and selection criteria can be used to screen potential crop border plant species and cultivars in the laboratory. It would be beneficial to the development of crop border plants to identify further such characteristics that

can be used to develop crop border selection criteria, taking aphid behavior into consideration as well as current farming practices.

Acknowledgments

We thank I. Millar (Biosystematics Division, ARC-Plant Protection Research Institute) for confirmation of the identity of *R. padi*, Goddy Prinsloo (ARC-SGI) for the *R. padi* culture, J. van den Berg (North West University) for supplying the maize seeds, OBARU for the wheat seeds and Rascal Seeds Research Laboratory (Pty) Ltd for the potato mini tubers, and I. Fourie (University of Pretoria) for laboratory assistance. Potatoes South Africa (PSA), the Technology and Human Resources for Industry Programme (THRIP), the National Research Foundation (NRF), and the University of Pretoria provided financial support.

References Cited

- Alla S., A. Cherqui, L. Kaiser, H. Azzouz, B. S. Sangwann-Norreel, and P. Giordanengo. 2003. Effects of potato plants expressing the nptII-gus fusion marker genes on reproduction, longevity, and host-finding of the peach-potato aphid, *Myzus persicae*. *Entomol. Exp. Appl.* 106: 95–102.
- AOAC. 2000. Official method of analysis 968.06, vol. 1. Association of Official Analytical Chemists, Arlington, VA.
- Barron, A. B. 2001. The life and death of Hopkins' host-selection principle. *J. Insect. Behav.* 14: 725–737.
- Bethke, J. A., R. A. Redak, and U. K. Schuch. 1998. Melon aphid performance on chrysanthemum as mediated by cultivar, and differential levels of fertilization and irrigation. *Entomol. Exp. Appl.* 88: 41–47.
- Boiteau, G. 1997. Comparative propensity for dispersal of apterous and alate morphs of three potato-colonizing aphid species. *Can. J. Zool.* 75: 1396–1403.
- Bradley, R. H. E. 1954. Studies of the mechanism of transmission of *Potato virus Y* by the green peach aphid, *Myzus persicae* (Sulz.) (Homoptera: Aphidae). *Can. J. Zool.* 32: 64–73.
- Bruce, T.J.A., L. J. Wadhams, and C. M. Woodcock. 2005. Insect host location: a volatile situation. *Trends Plant Sci.* 10: 269–274.
- DiFonzo, C. D., D. W. Ragsdale, E. B. Radcliffe, N. C. Gudmestad, and G. A. Secor. 1996. Crop borders reduce *Potato virus Y* incidence in seed potato. *Ann. Appl. Biol.* 129: 289–302.
- Farrell, J. A., and M. W. Stufkens. 1989. Flight activity and cereal host relationships of *Rhopalosiphum* spp. (Homoptera: Aphididae) in Canterbury. *New Zeal. J. Crop Hort.* 17: 1–7.
- Gorur, G., C. Lomonaco, and A. Mackenzie. 2007. Phenotypic plasticity in host choice behavior in black bean aphid, *Aphis fabae* (Homoptera: Aphididae). *Arthropod Plant Interact.* 1: 187–194.
- Guldmond, J. A. 1990. Choice of host plant as a factor in reproductive isolation of the aphid genus *Cryptomyzus* (Homoptera, Aphididae). *Ecol. Entomol.* 15: 43–51.
- Hokkanen, H. M. T. 1991. Trap cropping in pest management. *Annu. Rev. Entomol.* 36: 119–138.
- Hooks, C.R.R., and A. Fereres. 2006. Protecting crops from non-persistently aphid-transmitted viruses: a review on the use of barrier plants as a management tool. *Virus Res.* 120: 1–16.
- Hoxie, R. P., S. G. Wellso, and J. A. Webster. 1975. Cereal leaf beetle response to wheat trichome length and density. *Environ. Entomol.* 4: 365–370.
- Kennedy, J. S., and C. O. Booth. 1963. Free flight of aphids in the laboratory. *J. Exp. Biol.* 40: 67–85.
- Kennedy, J. S., C. O. Booth, and W.J.S. Kershaw. 1959. Host finding by aphids in the field II. *Aphis fabae* Scop. (Gynoparae) and *Brevicoryne brassicae* L.; with a re-appraisal of the role of host-finding behaviour in virus spread. *Ann. Appl. Biol.* 47: 424–444.
- Kennedy, J. S., C. O. Booth, and W.J.S. Kershaw. 1961. Host finding by aphids in the field III. Visual attraction. *Ann. Appl. Biol.* 49: 1–21.
- Leather, S. R., and A.F.G. Dixon. 1982. Secondary host preferences and reproductive activity of the bird cherry-oat aphid, *Rhopalosiphum padi*. *Ann. Appl. Biol.* 101: 219–228.
- Meier, U. 2001. Growth stages of mono- and dicotyledonous plants. BBCH monograph, 2nd ed. Federal Biological Research Centre for Agriculture and Forestry, Braunschweig, Germany.
- Minks, A. K., and P. Harrewijn. 1988. Aphids: their biology, natural enemies, and control. Elsevier, Netherlands.
- Müller, C. B., I. S. Williams, and J. Hardie. 2001. The role of nutrition, crowding and interspecific interactions in the development of winged aphids. *Ecol. Entomol.* 26: 330–340.
- Nault, B. A., D. A. Shah, H. R. Dillard, and A. C. McFaul. 2004. Seasonal and spatial dynamics of alate aphid dispersal in snap bean fields in proximity to alfalfa and implications for virus management. *Environ. Entomol.* 33: 1593–1601.
- Orlob, G. B. 1961. Host plant preference of cereal aphids in the field in relation to the ecology of barley yellow dwarf virus. *Entomol. Exp. Appl.* 4: 62–72.
- Payne, R., S. Welham, and S. Harding. 2012. A Guide to REML in GenStat®, 15th ed. VSN International, The Waterhouse, Waterhouse Street, Hertfordshire, UK.
- Pickett, J. A., L. J. Wadhams, C. M. Woodcock, and J. Hardie. 1992. The chemical ecology of aphids. *Annu. Rev. Entomol.* 37: 67–90.
- Ponder, K. L., J. Pritchard, R. Harrington, and J. S. Bale. 2001. Feeding behaviour of the aphid *Rhopalosiphum padi* (Homoptera: Aphididae) on nitrogen and water-stressed barley (*Hordeum vulgare*) seedlings. *Bull. Entomol. Res.* 91: 125–130.
- Powell, G. 1991. Cell membrane punctures during epidermal penetrations by aphids: consequences for the transmission of two potyviruses. *Ann. Appl. Biol.* 119: 313–321.
- Powell, G., R. Harrington, and N. J. Spiller. 1992. Stylet activities and *Potato virus Y* vector efficiencies by the aphids *Brachycaudus helichrysi* and *Drepanosiphum platanoidis*. *Entomol. Exp. Appl.* 62: 293–300.
- Powell, G., C. R. Tosh, and J. Hardie. 2006. Host plant selection by aphids: behavioral, evolutionary, and applied perspectives. *Annu. Rev. Entomol.* 51: 309–330.
- Radcliffe, E. B., and D. W. Ragsdale. 2002. Aphid-transmitted potato viruses: the importance of understanding vector biology. *Am. J. Potato Res.* 79: 353–386.
- Roberts, J. I., and J. E. Foster. 1983. Effect of leaf pubescence in wheat on the bird cherry oat aphid (Homoptera: Aphidae). *J. Econ. Entomol.* 76: 1320–1322.
- Schröder, M. L., and K. Krüger. 2014. Preference of aphids (Homoptera: Aphididae) for lucerne, maize, soybean and wheat and their potential as prospective border crops for *Potato virus Y* management in seed potatoes. *Afr. Entomol.* 22: 144–155.
- Sigvald, R. 1987. Aphid migration and the importance of some aphid species as vectors of *Potato virus Y^O* (PVY^O) in Sweden. *Potato Res.* 30: 267–283.
- Storer, J. R., J. S. Elmore, and H. F. Van Emden. 1993. Airborne volatiles from the foliage of three cultivars of autumn flowering chrysanthemums. *Phytochemistry* 34: 1489–1492.
- Storer, J. R., and H. F. van Emden. 1995. Antibiosis and antixenosis of chrysanthemum cultivars to the aphid *Aphis gossypii*. *Entomol. Exp. Appl.* 77: 307–314.
- Swenson, K. G. 1968. Role of aphids in the ecology of plant viruses. *Annu. Rev. Phytopathol.* 6: 351–374.
- Toba, H. H., A. N. Kishaba, G. W. Bohn, and H. Hield. 1977. Protecting muskmelons against aphid-borne viruses. *Phytopathology* 67: 1418–1423.
- Van Hoof, H. 1977. Determination of the infection pressure of *Potato virus Y^N*. *Neth. J. Plant Path.* 83: 123–127.
- Villanueva, B.J.R., and F. E. Strong. 1964. Laboratory studies on the biology of *Rhopalosiphum padi* (Homoptera: Aphidae). *Ann. Entomol. Soc. Am.* 57: 609–613.

Received 11 September 2014; accepted 30 April 2015.