

Visual cues and host-plant preference of the bird cherry-oat aphid, *Rhopalosiphum padi* (Hemiptera: Aphididae)

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Alate aphids respond to short (UV) and long (green–yellow) wavelength stimuli during host-plant searching behaviour. Although many aphids are attracted to yellow, the bird cherry-oat aphid, *Rhopalosiphum padi*, is attracted to green. As part of identifying suitable plant species for crop border plants for seed potatoes, the attraction of *R. padi* to different shades of green in relation to differences in spectral reflectance of three cultivars of a non-host, potato, and two host-plant species, maize and wheat, were determined. Choice experiments were carried out under laboratory conditions to evaluate aphid landing preference for stimuli of different colours. *Rhopalosiphum padi* alates preferred to land on the colour targets with the highest reflectance. Significantly more alates landed on yellow and lime colour targets with a maximum wavelength reflectance of 46 % from 600–610 nm and 26 % from 525–531 nm, respectively. The peak light reflectance of the crop plants ranged between 12 % (potato; 532–555 nm) and 20 % (wheat; 537–553 nm). The results on aphid landing preference for different colour targets suggest that *R. padi* will land in higher numbers on the wheat plants, compared to potato, due to their higher peak percentage reflectance. In addition, the study indicates that the wavelength reflectance curves of plants can be used as a characteristic to select possible crop border plants when making choices between seemingly equally suitable plant species/cultivars.

Key words: *Rhopalosiphum padi*, crop border plants, wavelength reflectance curves, maize, wheat, potato.

INTRODUCTION

Insect herbivores use visual and olfactory cues for host plant selection. Alate aphids (Hemiptera: Aphididae) respond to short (UV) and long (green–yellow) wavelength stimuli during the different phases of dispersion, and consequently landing and host-plant searching behaviour (Kennedy *et al.* 1961; Moericke 1962; Moericke 1969; Roach & Agee 1972). The autumn leaf colour co-evolutionary theory postulates that phytophagous insects, such as aphids, migrating to their primary host plant in winter prefer green leaves and dull hues of autumn colours (Hardie 1989; Archetti 2000; Archetti & Brown 2004). In contrast, autumn colours, such as red, serve as warning signals to herbivores (Archetti 2000). Besides evolutionary and ecological perspectives, the co-evolution theory has recently brought interest to the role of colour in aphid host-plant selection behaviour from an applied point of view.

Although several studies have found support for

the co-evolution theory of autumn colours (Archetti & Leather 2005; Ramírez *et al.* 2008), many of the studies did not take into account the perception of colour from the aphids' perspective (Schaefer & Rolshausen 2007). To address this problem, Döring *et al.* (2009) developed a colour choice model based on testing 70 different colours in the field, tentatively taking both aphid and human photoreceptor characteristics into account. The model indicated that aphids are able to distinguish between red and green leaves, with a tendency to avoid red. These findings were not species-specific and did not make any predictions of aphid colour preference in terms of different light intensities of green or yellow. For example, *Hyalopterus pruni* (Geoffroy) was attracted to unsaturated tints of orange-yellow-green with an optimum at yellow, whereas *Aphis fabae* (Scopoli) was more attracted to saturated tints that correspond to their respective host plants *Phragmites communis* (Poaceae) and *Beta vulgaris* (Chenopo-

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diaceae) (Moericke 1969). Furthermore, *Rhopalosiphum padi* (L.) was found to be attracted to green leaves of its primary host plant in autumn instead of trees with yellow leaves as predicted by the autumn co-evolution theory and the aphid colour preference model (Archetti & Leather 2005; Döring *et al.* 2009). These findings could be relevant for aphid control on agricultural crops.

A better understanding of the role of visual stimuli in aphid host plant selection behaviour could lead to improved aphid management, *e.g.* choice of trap colour and colour intensities for aphid monitoring and use of light reflectance to manage aphid-transmitted plant viruses (Döring & Chittka 2007). Many aphid species preferentially respond to yellow targets, and yellow traps are frequently used for aphid monitoring (Broadbent 1948; Heathcote 1957). However, yellow does not attract all aphid species to the same degree. For example, *Myzus persicae* (Sulzer) is more strongly attracted to yellow than are *Sitobion* species (Eastop 1955; Roach & Agee 1972). This could lead to skewed results where yellow-sensitive species are overestimated and species that are less sensitive to yellow are underestimated. Besides colour, the reflectance spectra of plant canopies affect aphid landing patterns. Whereas aphid composition and abundance in lime-green tile traps in soybean (*Glycine max* L., Fabaceae), resembling the reflectance spectra of the soybean canopy, correctly estimated aphid landing patterns compared to direct plant counts (Irwin 1980), the green tile trap overestimated aphid species colonizing pepper (*Capsicum annum*, L. Solanaceae) (Racah *et al.* 1985). Reflective mulches are another aphid management tool that rely on aphid vision (Döring & Chittka 2007). Silver reflective mulches have been found to delay the onset of *cucumber mosaic cucumovirus*, *watermelon mosaic I and II*, *zucchini yellows mosaic* and *squash mosaic* in summer squash (*Cucurbita pepo* L., Cucurbitaceae) and cantaloupe (*Cucumis melo* L., Cucurbitaceae) (Brown *et al.* 1993; Stapleton & Summers 2002).

The use of crop border plants has been proposed as an environmentally friendly method to reduce the spread of non-persistent viruses. Aphids tend to land in higher numbers at the edge of a field due to their sensitivity to the long wavelength light reflected from the soil and the contrasting plants (Broadbent *et al.* 1951; Swenson 1968; Minks & Harrewijn 1988). Planting a non-virus susceptible host plant around the edge of fields replaces the

edge and the crop border plant may act as a virus sink, a physical barrier or a trap plant (Hooks & Fereres 2006). Therefore, the choice of plant species used as a crop border plant is important and selecting a crop preferred by aphids may increase the edge effect and strengthen the crop border (Nault *et al.* 2004). For example, DiFonzo *et al.* (1996) showed that virus incidence in potato (*Solanum tuberosum* L., Solanaceae) was reduced when using soybean, maize (*Zea mays* L., Poaceae), potato and wheat (*Triticum aestivum* L., Poaceae) as crop border plants, although the use of potato is unfavourable since this is a virus source. In addition, the efficacy of crop border plants may differ depending on the plant species used. For example, grain sorghum (*Sorghum bicolor* L., Poaceae) was more effective in reducing incidence of *watermelon mosaic virus* and *papaya ringspot virus* than soybean and peanut (*Arachis hypogaea* L., Fabaceae) in the main crop pumpkin (*Cucurbita pepo* L., Cucurbitaceae) (Damicone *et al.* 2007).

Rhopalosiphum padi uses herbaceous plant species in the Poaceae as secondary host plants and is commonly found on cereals such as maize, wheat, barley (*Hordeum vulgare* L., Poaceae) and oat (*Avena sativa* L., Poaceae) (Dixon & Glen 1971; Leather 1993). Globally, *R. padi* is an economically important pest feeding on all the major cereal crops (Finlay & Luck 2011). In addition to causing major damage to cereal crops when occurring in high numbers, *R. padi* plays an important role in the transmission of non-persistent plant viruses such as *Potato virus Y* in seed potatoes (Dixon & Glen 1971; Radcliffe 1982). *Potato virus Y* causes considerable economic losses to seed potato growers in many parts of the world due to downgrading of seed lots (Radcliffe & Ragsdale 2002). The virus is mainly transmitted by migrating aphids in search of good-quality host plants (Boiteau 1997; Ragsdale *et al.* 2001). Non-persistent viruses can be acquired and transmitted within seconds after aphids alight on a plant. Non-colonizing or transient species alighting on non-host plants are thus able to transmit non-persistent viruses before taking off in search of a host plant (Radcliffe & Ragsdale 2002; Gray *et al.* 2010).

A previous study evaluated maize, wheat, soybean and lucerne (*Medicago sativa* L., Fabaceae) as potential crop border plants for aphids based on abundance and species composition in comparison with potato (Schröder & Krüger 2014). The findings suggested that in areas where cereal aphids

such as *R. padi* are abundant, maize and wheat have the potential to be used as crop border plants. The current study aims to determine if *R. padi* is attracted to different shades of green and to relate any preference for the spectral reflectance of three cultivars of the non-host, potato, as well as maize and wheat.

MATERIAL AND METHODS

Insects

A laboratory culture of *R. padi* was maintained on wheat plants in ventilated wooden cages with a top glass panel (55 × 45 × 35 cm), in a greenhouse ($T_{\text{Max}} = 24.8\text{ }^{\circ}\text{C}$; $T_{\text{Min}} = 10.3\text{ }^{\circ}\text{C}$; $\text{RH}_{\text{Max}} = 71.9\%$; $\text{RH}_{\text{Min}} = 26.8\%$) at the University of Pretoria. The culture was established with *R. padi* obtained from the Agricultural Research Council–Small Grain Institute (ARC-SGI), Bethlehem, South Africa. The original culture was established with aphids collected from wheat at Tygerhoek Experimental Farm, Riviersonderend, Western Cape (34°9'0"S 19°54'0"E) and supplemented with specimens collected from wheat in various wheat-growing regions in South Africa.

Alate aphids were obtained by crowding aphids on plants. Alates of varying ages actively flying or walking in the cage were collected for experiments.

Plants

Maize (cultivars 'CRN 3505', '6Q-121', '78-15B'), potato (cultivars 'BPI', 'Hertha', 'Mondial') and wheat (cultivars 'Duzi', 'Kariega', 'Krokodil') were grown from seed. Three maize seeds per pot (12.5 cm diameter) were planted, two potato mini tubers were placed in a pot and c. 20 wheat seeds were sown in two rows per pot, respectively. Pots contained an autoclaved soil mixture of river sand and coco peat in a ratio of 4:1. Slow release fertilizer (c. 1.6 g per pot; Grovida, Khula Kahle™ Fruit and Flower, N:P:K (3:1:5)), was added to the soil upon planting. From two weeks after planting, a foliar treatment of micronutrients (TREL MIX trace element solution) was applied to the plants weekly according to the manufacturer's instructions. The plants were grown at 25 °C with ambient relative humidity and a photoperiod of 16 h:8 h light:dark. Maize and wheat were used at plant growth stage 12 and 13 when two and three leaves were completely unfolded (Meier 2001). Potato plants were used at the plant growth stage 17 and 18 when seven and eight leaves had unfolded from the main stem (Meier 2001).

Aphid response to stimuli of different colours

Choice experiments were carried out in a glasshouse under natural light conditions and $T_{\text{Max}} = 24.8\text{ }^{\circ}\text{C}$; $T_{\text{Min}} = 10.3\text{ }^{\circ}\text{C}$; $\text{RH}_{\text{Max}} = 71.9\%$; $\text{RH}_{\text{Min}} = 26.8\%$, from May to June 2013. Colour cards consisted of circular sticky traps made from laminated cardboard, painted with a thin layer of insect glue (Plantex™) and placed in Petri dishes (13 cm in diameter). Five different shades of green cardboard were selected: lime-green (Sadipal, SIRIO™ 170 g), green (Sadipal, SIRIO™ 170 g), dark green (Elle Erre 220 g), olive-green (Grafton Paper Products 160 g) and mottled green (Mi-Teintes 160 g). In addition, white (Sadipal, SIRIO™ 170 g), yellow (Sadipal, SIRIO™ 170 g), grey (Mei-Teintes 160 g) and black (Grafton Paper Products 160 g) cardboard were included as controls. Different types of commercially available cardboard had to be selected due to the limited range of green intensities available within one type of cardboard. The colours were randomized within each trial and the Petri dishes were placed in a circle on a grey cement floor in an equidistant manner (Fig. 1). Experiments were carried out in ventilated insect cages (80 × 80 × 50 cm) covered with gauze. The cages, which were open at the bottom, were placed over the Petri dishes. Thirty-six aphids were released in the centre from an aluminium foil-covered podium (height 30 cm) in a cage. The number of aphids trapped on each colour card

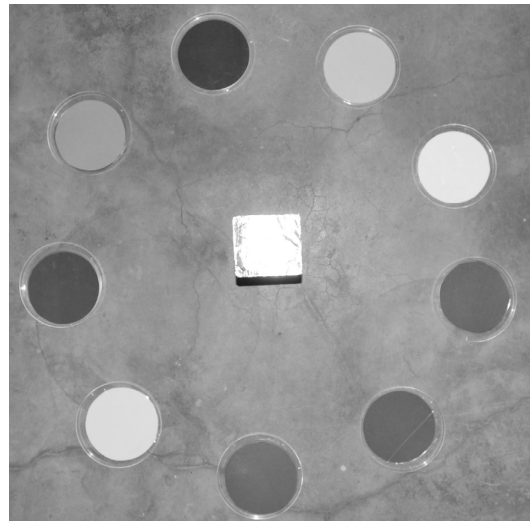


Fig. 1. Sticky colour card targets with five different shades of green, white, yellow, grey and black placed equidistantly in a circle on a grey background and an aluminium foil-covered release podium in the centre.

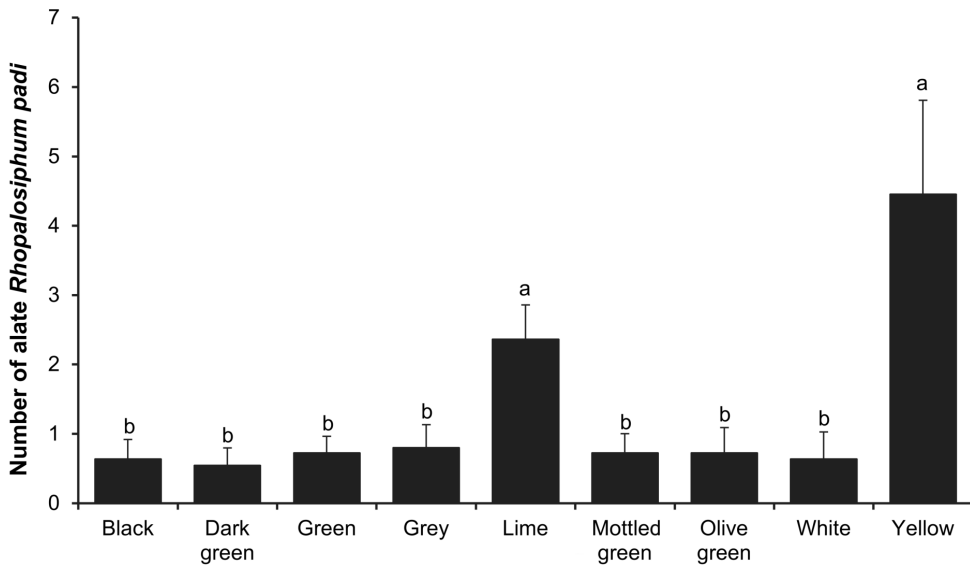


Fig. 2. Mean number (\pm S.E.) of *Rhopalosiphum padi* alates landing on sticky colour card models used as visual targets ($n = 11$; 36 aphids released per replicate). Different letters indicate significant differences ($P < 0.05$).

was counted after 24 hours. The experiment was replicated 11 times. Aphid counts were analysed with a generalized linear model one-way analysis of variance (ANOVA) with a Poisson distribution and a log link function. Means were separated using Fisher's least significant difference (LSD) test. Statistica[®] (Version 11 Statsoft, Inc. 1984–2012) was used for data analysis.

Spectral measurements

The percentage of light reflected by the sticky cards as well as the plants was measured with an AVANTES (Avaspec-3648) spectrophotometer with a deuterium-halogen light source (Avalight-DHc). A D65 light spectrum was used for the measurements and an AVANTES WS2 white tile as a white standard. The mean of the percentage of light reflected by the colour targets in the green–yellow spectrum (500–600 nm) was analysed with a one way ANOVA to determine statistical differences. Means were separated using Fisher's LSD. Statistica[®] (Version 11 Statsoft, Inc. 1984–2012) was used for data analysis.

RESULTS

The landing response of *R. padi* was significantly affected by the colour target (Wald = 95.98, d.f. = 8, $P < 0.01$). Significantly more *R. padi* alates landed on yellow (mean \pm S.E.: 4.45 ± 1.35) and

lime-green (2.36 ± 0.49) colour targets than on any of the other colour targets (Fig. 2). The number of alates landing on the yellow and lime-green targets did not differ significantly. In addition, there was no significant difference between the number of aphids landing on green, dark green, olive-green and mottled green, black, grey or white ($P > 0.05$).

The yellow colour card's peak percentage reflectance of 46 % ranged from 600 to 610 nm, whereas the peak percentage reflection of lime-green was 26 % at 525 and 531 nm, respectively. Green reflected 19 % and 15 % at 520 and 550 nm, respectively. The light reflectance curve of the dark green and olive-green was similar to the grey model's light reflectance curve, varying between 0 and 10 % across the UV-VIS light spectrum. Mottled green reflected less than 10 % light between 300 and 659 nm and increased to 12 % at 692 nm. White was saturated at 424–447 nm. The black and grey colour targets absorbed almost all light, reflecting 0–3 % and 0–7 % of light, respectively, across the UV-VIS spectrum (Fig. 3). Within the long wavelength region (green–yellow, 500–590 nm), grey, dark green and olive-green was not significantly different from one another. In contrast, yellow, lime-green, green, mottled green, white and black differed significantly from each other and from grey, dark green and olive-green in this wavelength region ($F_{8,18} = 856.8$, $P < 0.001$).

The light reflectance curve of wheat 'Duzi',

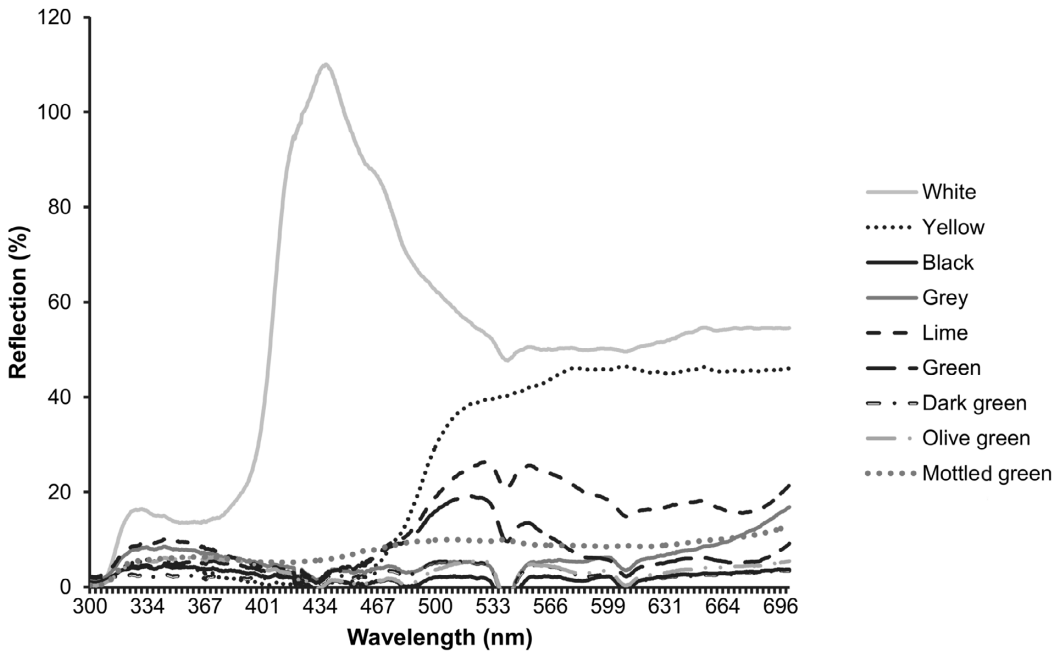


Fig. 3. Percentage light reflectance of the sticky colour cards.

'Kariega' and 'Krokodil' peaked between 537 and 553 nm, reflecting 18 %, 19 % and 20 % light, respectively. The peak percentage reflectance of the three maize cultivars was between 531 and 556 nm, with maize '6Q-121' reflecting the highest percentage of light (14 %) and maize '78-15B' and 'CRN 3505' each reflecting 12 % of light at the peak. Potato 'BP1' and 'Mondial' reflected 13 % and potato 'Hertha' 15 % of light at the peak of the reflectance curve between 532 and 555 nm (Fig. 4).

DISCUSSION

Rhopalosiphum padi preferred light intensities of the yellow and lime-green coloured cards to the darker shades of green tested, with similar number of alates landing on the yellow and the lime-green cards. Our results are in line with those of Roach & Agee (1972), who observed that *R. padi* summer morphs preferred yellow (Sherwin-Williams Solar Yellow) to green (Sherwin-Williams Vibrant Green). The attraction of *R. padi* to lime-green indicates that this species may be able to distinguish between different intensities of green as well as grey, white and black. The lack of attractiveness of white confirms that, like for other aphid species (Kennedy *et al.* 1961; Moericke 1962), *R. padi* prefers long (green–yellow) to short (UV) wavelength

light during the alighting phase, as demonstrated in field experiments by A'Brook (1973). The fact that few alates landed on black, grey and the darker shades of green also suggests that *R. padi* requires reflective targets for attraction.

The percentage of light reflected from plants and colour traps play an important role in wavelength discrimination in aphids (Moericke 1955; Kennedy *et al.* 1961). Roach & Agee (1972) suggested that the higher number of *R. padi* alates caught in yellow compared to green traps was due to the increased brightness of the yellow traps reflecting light at a peak of 100 % whereas the green traps reflected light at a peak of 45 %. Eastop (1955) showed that the preference of yellow observed for *R. maidis* (Fitch) varied with the intensity of sunlight, emphasizing that light intensity (percentage light reflected) may be an important cue in host plant choice. Likewise, Moericke (1969) found that intensity was an important cue for *H. pruni*, which preferred dull hues of yellow over other hues. Similarly, light intensity is an important cue for *R. padi*, which preferred to land on targets with the highest percentage reflectance in the long wavelength region, in our study.

Kennedy *et al.* (1961) proposed that the main function of colour vision in aphids is to distinguish between light reflected from the sky and the

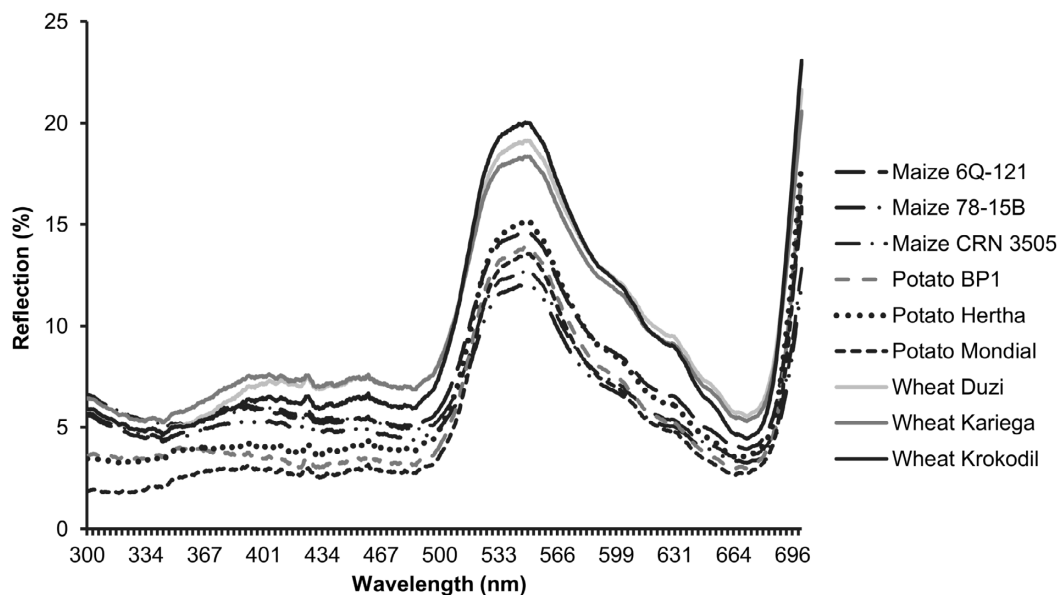


Fig. 4. Percentage light reflectance of leaves from three maize, potato and wheat cultivars each.

plants. During the first phase of dispersal/distance flight, aphids are attracted to short wavelength light, *i.e.* UV light reflected from the sky, and do not respond to long wavelengths reflected by green or yellow foliage. This behaviour changes during low-level/short-distance flight when aphids become responsive to long wavelength light (Moericke 1955). Subsequently, it has been suggested that aphids use the ratio between long and short wavelength light to navigate between plants rather than responding to only the one or the other (Kennedy *et al.* 1961; Kennedy & Booth 1963). Döring & Chittka (2007) also argued that the yellow preference shown by aphids should not be viewed as a true colour preference but rather a response that is dependent on the actual light intensity. The yellow preference observed for some aphid species, including summer morphs of *R. padi*, may be due to yellow representing a superfoliage stimulus to herbivorous insects rather than it being an ecological adaptation (Prokopy & Owens 1983). Yellow may stimulate the opponent processing mechanisms thought to be involved in aphid colour vision stronger than green does, because yellow reflects more light in the long wavelength region (green to red) than in the short wavelength region (UV to blue), resulting in a greater excitation of the opponent mechanism than with green (Döring & Chittka 2007).

Our results contradict previous findings where

R. padi was shown to prefer green over yellow (Kieckhefer *et al.* 1976; Archetti & Leather 2005). Kieckhefer *et al.* (1976) found that *R. padi* was more frequently attracted to green compared to yellow in an experiment where coloured photographic filters were used as colour stimuli. However, in their study fluorescent and incandescent bulbs supplied light, and the yellow light had a higher intensity than the green light. Archetti & Leather (2005) counted aphids directly on the leaves of *Prunus padus* (Rosaceae), the primary host plant, and did not measure the wavelength reflectance of the leaves. Light intensity (dull green/bright yellow) was therefore not tested unambiguously and olfactory cues emitted by the host plants likely played an important role in host plant selection. The difference found in the light intensity preference between these and our study could also be due to the aphid morph used in experiments.

Heteroecy causes different aphid morphs to behave differently towards the same host plant cues, including wavelength reflectance, depending on the phase of the life cycle (Dixon 1971; A'Brook 1973; Leather & Dixon 1982; Glinwood & Pettersson 2000). Autumn co-evolutionary studies have focused on autumn aphid morphs that migrate from the secondary host plant to the primary host plant to mate, oviposit and overwinter in the egg stage. Agricultural studies are generally performed with the summer morph that colonizes herbaceous

plants, such as crops, and reproduces parthenogenetically. Heteroecious species that feed on secondary herbaceous plants during summer tend to have a greater sensitivity for brighter colours such as yellow (Eastop 1955; Heathcote 1957; Kennedy *et al.* 1961). Furthermore, autumn and summer morphs of aphids display morphological and behavioural differences (Leather & Dixon 1982; Leather *et al.* 1983; Simon *et al.* 1991). Spring emigrants and summer virginoparae display distinct host plant preferences. Once the behavioural change has occurred to migrate to the secondary host, the emigrants will not return to the primary host plant (Glinwood & Pettersson 2000). It is possible that the summer morphs of *R. padi* used in our study are more sensitive to brighter colours such as yellow than the autumn morphs which preferred the more dull green in the study by Archetti & Leather (2005).

It has been shown that wavelength reflectance of plant leaves can be of importance for alighting *Brevicoryne brassicae* L., which were more strongly attracted to wavelength reflectance of sugar beet leaves (*Beta vulgaris* L., Chenopodiaceae), a non-host, compared to cabbage (*Brassica oleraceae* L., Brassicaceae), a preferred host plant (Kennedy *et al.* 1961). The spectral reflectance of cabbage leaves showed that they reflected more light in the short wavelength (UV) region than the sugar beet leaves (Kennedy *et al.* 1961). Another example is *H. pruni*, which alighted in greater numbers on leaves of its summer host *Phragmites communis* L. (Poaceae) than on leaves of sugar beet (Moericke 1969). These studies suggest that plant leaf colour may affect aphid landing rates. There was little difference in the peak reflectance of maize, potato and wheat in our study. The results of the colour choice experiment suggest that *R. padi* will land in higher numbers on the wheat plants, due to their higher peak percentage reflectance (20 %) compared to the maize and potato cultivars. However, a landing preference study showed no difference in the number of *R. padi* landing on maize and wheat (Schröder *et al.*, in prep), suggesting that other cues also play a role.

Understanding aphid vision is a key aspect in

the selection of crop border plants. Aphids are known to respond to the contrast in long and short wavelength light reflected by the brown-green interface at the edge of a crop field (Kennedy *et al.* 1961; Minks & Harrewijn 1988). Aphids therefore land in higher numbers at the edge of a crop because they become more sensitive to long wavelength than short wavelength light in the alighting phase (Kennedy *et al.* 1961). Our study demonstrates that *R. padi* is able to distinguish between different intensities of green, based on the percentage of light reflected in the green/long wavelength region. In addition, plants that reflect a higher percentage of light in the green region, such as the wheat plants measured in the present study, may be more attractive compared to plants reflecting a low percentage of light in the green region due to an increase in short/long wavelength light. Therefore, wheat is promising as a good crop border plant for seed potatoes to reduce PVY transmission as it reflected the highest percentage of light in the long wavelength region compared to maize and potato. The study suggests that plant wavelength reflectance can be used as a characteristic to select crop border plants and that the plant to be used for the crop border should reflect a higher percentage of light in the long wavelength region than the main crop.

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