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Plant quality vs. risk of parasitism: within-plant distribution and performance of the corn leaf aphid, *Rhopalosiphum maidis*

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Abstract

1 Colonies of the aphid *Rhopalosiphum maidis* on Johnsongrass, *Sorghum halepense*, usually occur inside the whorl. The present work assessed the role of two biotic factors, plant quality and parasitism by *Lysiphlebus testaceipes*, in determining within-plant distribution and performance of *R. maidis*. The mean relative growth rate of aphids inside the whorl and on a mature leaf was compared, and the concentration of hydroxamic acids in those tissues determined as an indicator of plant quality. Parasitism effectiveness and parasitoid behaviour were evaluated using three treatments: aphid colonies placed (1) wholly inside the whorl, (2) on the inner and outer surfaces of the whorl, and (3) on a mature leaf.

2 The mean relative growth rate of aphids was lower on the whorl than on the mature leaf, and hydroxamic acid concentration in the whorl was higher than in the mature leaf.

3 The number of parasitized dead aphids (mummies) inside the whorl was considerably lower than in the other two treatments. Mummies were present in 80% of the replicates in the whorl, whereas mummies were present in all replicates of the other treatments.

4 Host location time of the parasitoid was increased on the mature leaf compared with the other treatments. No significant differences in the residence time of the parasitoid in the aphid colony occurred between treatments.

5 Host location time showed a negative correlation, and residence time of the parasitoid a positive correlation with the number of aphids on the outer surface of the whorl.

Keywords Aphids, hydroxamic acids, *Lysiphlebus testaceipes*, parasitoids, plant quality, *Rhopalosiphum maidis*, *Sorghum halepense*.

Introduction

The nutritional composition of plants, e.g. soluble nitrogen and carbohydrates, and their levels of defensive secondary metabolites vary substantially from one tissue to another (Raupp & Denno, 1983; Rosenthal & Berenbaum, 1991). The parts of plants on which aphids feed may therefore differ in their quality as substrates for the development of aphid populations (Whitham, 1980). On the other hand, specific structures of the plant may enable aphids to escape the attack of predators (Kareiva & Sahakian, 1990; Grevstad & Klepetka, 1992) and parasitoids (Gardner & Dixon, 1985; Reed *et al*., 1992), thereby providing refuges for these phytophagous insects (Price, 1980, 1988). Thus, plant traits as well as interactions between biotic and abiotic factors may affect aphid performance (Morris, 1992) and within-plant aphid distribution (Jansson & Smilowitz, 1986; Lampert, 1989).

The corn leaf aphid, *Rhopalosiphum maidis* (Fitch), is a common pest of cereals such as maize, sorghum and barley (Ortega *et al*., 1980). This aphid also colonizes wild Gramineae (Poaceae) in the surroundings of crops (Blackman & Eastop, 1984). Colonies of *R. maidis* in maize are usually found inside the whorl formed by the youngest leaves of the plant, occupying outer positions only when the size of the colony increases beyond a threshold level or after the plant grows and the tassel becomes exposed (Foott, 1977). In sorghum, *R. maidis* colonies have also been found in the whorl (Gonzáles, personal observation). *Rhopalosiphum maidis* is attacked in the field by predacious Coccinelidae (Coleoptera) and Syrphidae (Diptera) (Frazer,

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1987) and is parasitized by Braconidae (Hymenoptera) (Starý, 1987; Feng *et al*., 1992).

In preliminary field observations, colonies of *R. maidis* were found on mature plants of the common weed Johnsongrass, *Sorghum halepense* (L.) Pers., in the vicinity of wheat crops in Santiago, Chile (late spring, November 1996). All infested plants ($n = 47$) had aphid colonies in the whorl, and only four of these plants had an additional colony outside of the whorl. Most aphids, both inside and outside the whorl, were found on the abaxial surface of leaves. The percentage of mummies was lower in the colonies inside the whorl (1%) than in those outside it (12%). The braconid *Lysiphlebus testaceipes* (Cresson) was the only parasitoid species emerging from the collected mummies.

In the present work, the role of plant quality and the risk of parasitism in shaping the within-plant distribution pattern of *R. maidis* were investigated. The performance of aphids in the whorl and on a mature leaf of Johnsongrass were evaluated. In addition, the concentration of hydroxamic acids, defensive secondary metabolites of Poaceae (Niemeyer, 1988; Niemeyer & Pérez, 1995), within those plant tissues was determined. Finally, the effect of feeding site of aphids on the risk of parasitism by *L. testaceipes*, a generalist parasitoid of aphids (Starý *et al*., 1988), was addressed.

Materials and Methods

Stock cultures and plant material

Cultures of *R. maidis* and *L. testaceipes* originally collected in 1996 from Johnsongrass in Santiago, Chile, were maintained on barley (*Hordeum vulgare* L. cultivar F. Union). Barley lacks hydroxamic acids (Niemeyer, 1988). Cultures were maintained in a room at 25 ± 2 °C and a photoperiod of LD 14 : 10 h. All experiments were performed using Johnsongrass (5–7-week-old plants) grown from seed outdoors during the austral summer and autumn months (24 ± 8 °C and 11–14 h of light per day).

Aphid performance

Second-instar nymphs born within a 12-h period were placed inside plastic clip cages (2 cm diameter × 2 cm height) attached to the following parts of each plant: (1) abaxial surface of the youngest leaf (within the whorl), and (2) abaxial surface of a mature leaf (fourth or fifth oldest leaf in a plant with seven or eight leaves). The youngest leaf was carefully extended to allow the clip cage to be attached. Neither chlorosis nor symptoms of damage were observed on both young and mature leaves after the 4 days of experimentation. Mean relative growth rate of aphids (MRGR; Adams & Van Emden, 1972) was determined as a measure of the performance of individual aphids. Thirty nymphs were each weighed (initial weight: 15–20 µg) and then individually caged on both plant sites studied (one cage per plant site). Aphids were removed from the clip cages after 4 days and weighed. MRGRs [(ln final weight – ln initial weight)/number of days] for each site were compared using a Wilcoxon matched pairs test, as the data did not fit a normal distribution and both sites belonged to the same plant in each replicate ($n = 15$ plants).

Analysis of secondary metabolites

Hydroxamic acids were quantified in the youngest leaf and in a mature leaf (fourth or fifth oldest leaf in a plant with seven or eight leaves) using a modification of the HPLC method developed by Niemeyer *et al*. (1989). A sample (150–250 mg) of each plant part ($n = 16$ plants) was macerated with 1 mL distilled water, using a mortar and pestle. The aqueous extract was left at room temperature for 15 min and then taken to pH 3 with 0.1 N H_3PO_4. The extract was centrifuged at 13 000 g for 15 min and a 50 µL aliquot of the supernatant directly injected into a high performance liquid chromatograph. A RP-100 Lichrospher-C18 column was used with a constant solvent flow of 2 mL/min and the following linear gradients between solvents A (MeOH) and B (0.5 mL H_3PO_4 in 1 L H_2O): 0–1.5 min, 5% A; 1.5–5 min, 30% A; and then constant 30% A to 9 min. Detection of DIBOA, the main hydroxamic acid aglucone present in the extracts, was performed at 263 nm, its retention time being 7.5 min with a 0.05 min range. Results were compared using a Wilcoxon matched pairs test for the reasons given in the preceding section.

Evaluation of parasitism

The experiment consisted of three treatments using Johnsongrass plants (initial $n = 15$ in each treatment), and was performed in a room at 25 ± 2 °C, photoperiod LD 14 : 10 h, and 48 W/m^2 total radiation from incandescent and fluorescent white lamps. Ninety adult aphids of similar size were placed with a fine camelhair brush on each of the following plant sites: (1) inside the whorl, (2) distributed between the inner and the outer surface of the whorl (between 10 and 40 aphids being located on the outer surface of the whorl), and (3) on the mature leaf. Aphids had to be confined in clip cages for the first 30 min to assure settlement in the treatments. After approximately 3 h no further aphid movements occurred between sites. At this point, approximately 80 aphids had settled at each plant site (Table 2). Each infested plant was then isolated using a plastic tube (40 cm diameter × 75 cm height) and a mated female parasitoid was released next to the base of the plant. Parasitoid behaviour was then observed continuously for 5 h, noting when its location in the plant changed. 'Host location time' was defined as the time elapsed from the release of the parasitoid to the first observation of the parasitoid amongst the aphid colony, and 'residence time' as the accumulated time the parasitoid was observed within the aphid colony. At the end of the observation period, the parasitoid was removed and each group of aphids was transferred to isolated barley seedlings located in the same room. The resulting number of mummies was counted 10–12 days later. A colony was labelled as 'parasitised' when at least one mummy was found in it. Three replicates from the treatment wholly inside the whorl were accidentally lost, therefore the sample size for this treatment was $n = 12$. Results were compared using a Kruskal–Wallis ANOVA because data did not fit a normal distribution. Correlations (Spearman Rank Order correlations) between both host location and residence times and the number of aphids outside the whorl were determined for the treatment distributed between the inner and the outer part of the whorl. This was done just for this treatment because it was the only one

encompassing variation in the number of aphids available for parasitization (i.e. in the size of the aphid patch).

Results

Aphid performance and analysis of secondary metabolites

MRGR of *R. maidis* on the youngest leaf was significantly lower (Wilcoxon matched pairs test, $Z = 2.31$, $P < 0.05$) than on the mature leaf of the same plant (Table 1). The leaves also differed in hydroxamic acid concentration, the youngest leaf having a higher concentration (Wilcoxon matched pairs test, $Z = 4.73$, $P < 0.01$) than did the mature leaf (Table 1).

Evaluation of parasitism

Parasitoids showed an initial tendency to move upwards, irrespective of the position of aphids on the plant. Thus, in both treatments where aphids were located on the top of the plant (either wholly or partially inside the whorl) the sequence of leaves contacted by the parasitoid, which was released next to the base of the plant, indicated a straightforward movement to the upper leaves, with no backward movements. This was observed for 14 out of 15 parasitoids in the treatment with aphids partially inside the whorl, and all 12 parasitoids in the treatment with aphids wholly inside it. In the case of the treatment on the mature leaf (a lower leaf), 13 out of 15 parasitoids initially 'overlooked' the aphid colony on their way to the top and found it only after downward movements.

Inside the whorl, 12 of the 15 aphid colonies were parasitized, in contrast to the other treatments where all aphid colonies were parasitized (Table 2). Host location time by the parasitoid on the mature leaf was significantly longer (Kruskal–Wallis ANOVA, $H(2,42) = 18.96$, $P < 0.001$) than in the other treatments (Table 2).

Table 1 Mean Relative Growth Rate (MRGR) of individuals of *R. maidis* on the youngest leaf and on a mature leaf of Johnsongrass, and hydroxamic acid levels (Hx) in those tissues[a].

Plant part	MRGR ($mg/g.day^{-1}$) ($n = 15$)	Hx (mmol/kg fresh weight) ($n = 16$)
Young leaf	0.397 ± 0.015a	3.88 ± 0.54a
Mature leaf	0.438 ± 0.012b	2.17 ± 0.35b

[a] Means followed by a different letter within a column are significantly different, Wilcoxon matched pairs test ($P < 0.05$). Mean ± SE shown.

There was no significant difference in residence time among treatments (Kruskal–Wallis ANOVA, $H(2,42) = 4.25$, $P = 0.12$; Table 2). The number of mummies found in the parasitized colonies inside the whorl was significantly lower (Kruskal–Wallis ANOVA, $H(2,42) = 27.05$, $P < 0.0001$) than in the other two treatments (Table 2). Host location time by the parasitoid showed a negative correlation ($n = 15$, $r = -0.761$, $P < 0.001$) and residence time in the aphid colony a positive correlation ($n = 15$, $r = 0.713$, $P < 0.01$) with the number of aphids established outside of the whorl.

Discussion

Plant suitability for aphids normally changes with plant and tissue age (Leather & Dixon, 1981; Wiktelius, 1987), the changes affecting aphid feeding and nutrition (Klingauf, 1987). Younger leaves usually have a higher concentration of primary metabolites, e.g. soluble nitrogen, than mature ones (Merritt, 1996; Dixon, 1998;: p. 38). Therefore, assuming this pattern to hold in the present system, an enhanced aphid performance on younger leaves would be expected. However, aphid growth rate was lower on the whorl (youngest leaves) than on a mature leaf. This suggests the involvement of non-nutritional factors in the leaves. The concentration of hydroxamic acids was higher in the whorl. Previous work has reported negative correlations between performance of *R. maidis* and concentration of hydroxamic acids in Poaceae (Long *et al*., 1977; Givovich & Niemeyer, 1994). The same pattern has been found for other cereal aphids in laboratory bioassays (Bohidar *et al*., 1986; Thackray *et al*., 1990; Givovich & Niemeyer, 1995) and in the field (Gianoli *et al*., 1996). The concentration of hydroxamic acids depends on the plant structure assayed and its age (Argandoña *et al*., 1981), being higher in younger leaves than in mature ones. Consequently, these results suggest that hydroxamic acid concentration in Johnsongrass leaves could be a factor accounting for the MRGR values determined for *R. maidis*. It may be hypothesized that the effect of chemical defences might have overcome the presumably richer nutrient composition of the whorl (Langer, 1979; Dixon, 1998), resulting in a negative effect on aphid performance.

Results of the present study further suggest that the whorl may be regarded as a sheltered environment for aphids. Previous studies have indicated that natural enemies of aphids, such as coccinellids and parasitoids, are inefficient in finding prey in concealed environments such as the leaf-rolling caused by the Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Reed *et al*., 1992; Kauffman & Laroche, 1994). In the present case, the level

Table 2 Evaluations of parasitism of *R. maidis* by *L. testaceipes* [a]; WI = all aphids inside the whorl, WIO = aphids located both on the inner and outer surfaces of the whorl, ML = all aphids located on a mature leaf. Means ± SE are given.

Treatment	Number of plants (colonies)	Number of aphids per colony	Colonies parasitized	Host location time (min)	Residence time (min)	Number of mummies in parasitized colonies
WI	15	82 ± 1a	12	38.8 ± 4.0a	51.3 ± 4.2a	3 ± 1a
WIO[b]	15	81 ± 1a	15	31.4 ± 4.1a	68.1 ± 7.4a	17 ± 2b
ML	15	79 ± 1a	15	73.3 ± 7.1b	66.1 ± 4.4a	22 ± 1b

[a] Means followed by a different letter within a column are significantly different (Kruskal–Wallis ANOVA, $P < 0.001$).
[b]The mean number of aphids (± SE) inside the whorl was 58 ± 3 and outside the whorl was 22 ± 3.

of parasitism was lowest inside the whorl. This advantage could counterbalance the deleterious effect for aphids of settling in a plant site where development is hindered, and could explain the distribution pattern of *R. maidis* colonies found in the field. The most disadvantageous location for colonies of *R. maidis* on Johnsongrass is therefore the outer surface of the whorl, where intrinsic plant factors limit aphid growth and the aphids are easily discovered and attacked by parasitoids.

In support of a previous report on the behaviour of *L. testaceipes* (Städler & Völkl, 1991), parasitoids in the treatment with all aphids inside the whorl foraged principally at the edge of the aphid colony and spent little time in secluded plant areas. Consequently, the number of mummies inside the whorl were lower than in the other treatments, despite the fact that residence times were not different. On the other hand, even though the parasitoids were released next to the base of the plant, they showed a marked orientation towards the apex, therefore finding the aphid colonies located on the whorl before those located on the mature leaf. Thus, parasitoid behaviour would explain why the large mature leaf, a presumably more 'apparent' site (*sensu* Feeny, 1976), was not associated with a shorter host location time.

The results indicate that the whorl plays two important but contrasting roles for the corn leaf aphid: (1) as a structural refuge against natural enemies, and (2) as a low quality substrate. The system is a dynamic one. It can be expected that as aphid number increases, the limited space inside the whorl and the growth of the plant will expose them to parasitoid attacks, as indicated by the correlations obtained between both host location and residence times and number of aphids outside of the whorl. This would exert a pressure on aphids to reach the newly formed whorl, where, in spite of the fact that their growth will be reduced, they would gain protection from parasitoids, i.e. they would reach an 'enemy-free space' (Jeffries & Lawton, 1984; Hopkins & Dixon, 1997).

This work provides some insights into the pattern of within-plant distribution of *R. maidis* and the potential trade-offs between plant quality and protection against parasitoids. Further work should also consider other factors, such as the presence of predators (e.g. coccinellids) or mutualists (e.g. attendant ants), and possible roles of the whorl as protection against extreme environmental conditions.

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References

Adams, J.B. & van Emden, H.F. (1972) Biological properties of aphids and their host plant relationships. *Aphid Technology* (ed. by H. F. van Emden), pp. 48–97. Academic Press, London.

Argandoña, V.H., Niemeyer, H.M. & Corcuera, L.J. (1981) Effect of content and distribution of hydroxamic acids in wheat on infestation by the aphid *Schizaphis graminum*. *Phytochemistry*, **20**, 673–676.

Blackman, R.L. & Eastop, V.F. (1984) *Aphids on the World's Crops*. Wiley, New York.

Bohidar, K., Wratten, S.D. & Niemeyer, H.M. (1986) Effects of hydroxamic acids on the resistance of wheat to the aphid *Sitobion avenae*. *Annals of Applied Biology*, **109**, 193–198.

Dixon, A.F.G. (1998) *Aphid Ecology*. 2nd edn. Chapman & Hall, London.

Feeny, P. (1976) Plant apparency and chemical defenswe. *Biochemical Interactions Betweeen Plants and Insects* (ed. by J. W. Wallace and R. L. Mansell), pp. 1–40. Plenum Press, New York

Feng, M.G., Johnson, J.B. & Halbert, S.E. (1992) Parasitoids (Hymenoptera: Aphidiidae and Aphelinidae) and their effect on aphid (Homoptera: aphididae) populations in irrigated grain in Southwestern Idaho. *Environmental Entomology*, **21**, 1433–1440.

Foott, W.H. (1977) Biology of the corn leaf aphid, *Rhopalosiphum maidis* (Homoptera: Aphididae), in Southwestern Ontario. *The Canadian Entomologist*, **109**, 1129–1135.

Frazer, B.D. (1987) Predators. *Aphids: Their Biology, Their Enemies and Control*, Vol. 2B (ed. by A. K. Minks and P. Harrewijn), pp. 217–230. Elsevier, Amsterdam.

Gardner, S.H. & Dixon, A.F.G. (1985) Plant structure and the foraging success of *Aphidius rhopalosiphi* (Hymenoptera: Aphididae). *Ecological Entomology*, **10**, 171–179.

Gianoli, E., Papp, M. & Niemeyer, H.M. (1996) Costs and benefits of hydroxamic acid-related resistance in winter wheat against the bird cherry-oat aphid, *Rhopalosiphum padi* L. *Annals of Applied Biology*, **129**, 83–90.

Givovich, A. & Niemeyer, H.M. (1994) Effect of hydroxamic acids on feeding behaviour and performance of cereal aphids (Hemiptera: Aphididae) on wheat. *European Journal of Entomology*, **91**, 371–374.

Givovich, A. & Niemeyer, H.M. (1995) Comparison of the effect of hydroxamic acids from wheat on five cereal aphids. *Entomologia Experimentalis et Applicata*, **74**, 115–119.

Grevstad, F.S. & Klepetka, B.W. (1992) The influence of plant architecture on the foraging efficiencies of a suite of ladybird beetles feeding on aphids. *Oecologia*, **92**, 399–404.

Hopkins, G.W. & Dixon, A.F.G. (1997) Enemy-free space and the feeding niche of an aphid. *Ecological Entomology*, **22**, 271–274.

Jansson, R.K. & Smilowitz, Z. (1986) Influence of nitrogen on population parameters of potato insects: abundance, population growth, and within-plant distribution of the green peach aphid, *Myzus persicae* (Homoptera: Aphididae). *Environmental Entomology*, **15**, 49–55.

Jeffries, M.J. & Lawton, J.H. (1984) Enemy-free space and the structure of ecological communities. *Biological Journal of the Linnean Society*, **23**, 269–286.

Kareiva, P. & Sahakian, R. (1990) Tritrophic effects of a simple architectural mutation in pea plants. *Nature*, **345**, 433–434.

Kauffman, W.C. & Laroche, S.L. (1994) Searching activities by coccinellids on rolled wheat leaves infested by the Russian wheat aphid. *Biological Control*, **4**, 290–297.

Klingauf, F.A. (1987) Host plant finding and acceptance. *Aphids: Their Biology, Their Enemies and Control*, Vol. 2A (ed. by A. K. Minks and P. Harrewijn), pp. 225–253. Elsevier, Amsterdam.

Lampert, E.P. (1989) Seasonal abundance and within-plant distribution of aphids (Homoptera: Aphididae) on flue-cured tobacco. *Journal of Economic Entomology*, **82**, 114–118.

Langer, R.H.M. (1979) *How Grasses Grow*. Edward Arnold, London.

Leather, S.R. & Dixon, A.F.G. (1981) The effect of the cereal growth stage and feeding site on the reproductive activity of the bird-cherry

aphid, *Rhopalosiphum padi*. *Annals of Applied Biology*, **97**, 135–141.

Long, B.J., Dunn, G.M., Bowman, J.S. & Routley, D.G. (1977) Relationship of hydroxamic acid content in corn and resistance to the corn leaf aphid. *Crop Science*, **17**, 55–58.

Merritt, S.Z. (1996) Within-plant variation in concentrations of amino acids, sugar, and sinigrin in phloem sap of black mustard, *Brassica nigra* (L.) Koch (Cruciferae). *Journal of Chemical Ecology*, **22**, 1133–1145.

Morris, W.F. (1992) The effects of natural enemies, competition, and host plant water availability on an aphid population. *Oecologia.*, **90**, 359–365.

Niemeyer, H.M. (1988) Hydroxamic acids (4-hydroxy-1,4-benzoxazin-3-ones), defence chemicals in the Gramineae. *Phytochemistry*, **27**, 3349–3358.

Niemeyer, H.M. & Pérez, F.J. (1995) Potential of hydroxamic acids in the control of cereal pests, diseases, and weeds. *Allelopathy. Organisms, Processes, and Applications* (ed. by K. M. M. Inderjit, Dakshini and F.A.Einhellig), pp. 260–269. ACS Symposium Series 582, Washington, D.C.

Niemeyer, H.M., Pesel, E., Copaja, S.V., Bravo, H.R., Franke, S. & Francke, W. (1989) Changes in hydroxamic acid levels of wheat plants induced by aphid feeding. *Phytochemistry*, **28**, 447–449.

Ortega, A., Vasal, S.K., Mihm, J. & Hershey, C. (1980) Breeding for insect resistance in maize. *Breeding Plants Resistant to Insects* (ed. by F. G. Maxwell and P. R. Jennings), pp. 371–419. Wiley, New York.

Price, P.W. (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics*, **11**, 41–65.

Price, P.W. (1988) Inversely density-dependent parasitism: the role of plant refuges for hosts. *Journal of Animal Ecology*, **57**, 89–96.

Raupp, M.J. & Denno, R.F. (1983) Leaf age as a predictor of herbivore distribution and abundance. *Variable Plants and Herbivores in Natural and Managed Systems* (ed. by R. F. Denno and M. S. McClure), pp. 91–124. Academic Press, New York.

Reed, D.K., Kindler, S.D. & Springer, T.L. (1992) Interactions of Russian wheat aphid, a hymenopterous parasitoid and resistant susceptible slender wheatgrasses. *Entomologia Experimentalis et Applicata*, **64**, 239–246.

Rosenthal, G.A. & Berenbaum, M.R. (1991) *Herbivores: Their Interactions with Secondary Plant Metabolites*, Vol. I. 2nd edn. Academic Press, San Diego.

Städler, B. & Völkl, W. (1991) Foraging pattern of two aphid parasitoids, *Lysiphlebus testaceipes* and *Aphidius colemani* on banana. *Entomologia Experimentalis et Applicata*, **58**, 221–229.

Starý, P. (1987) Aphidiidae. *Aphids: Their Biology, Their Enemies and Control*, Vol. 2B (ed. by A. K. Minks and P. Harrewijn), pp. 171–184. Elsevier, Amsterdam.

Starý, P., Lyon, J.P. & Leclant, F. (1988) Post-colonisation host range of *Lysiphlebus testaceipes* in the mediterranean area (Hymenoptera: Aphidiidae). *Acta Entomologica Bohemoslovaca*, **85**, 1–11.

Thackray, D.J., Wratten, S.D., Edwards, P.J. & Niemeyer, H.M. (1990) Resistance to the aphids *Sitobion avenae* and *Rhopalosiphum padi* in Gramineae in relation to hydroxamic acid levels. *Annals of Applied Biology*, **116**, 573–582.

Whitham, T.G. (1980) The theory of habitat selection: examined and extended using *Pemphigus* aphids. *American Naturalist*, **115**, 449–466.

Wiktelius, S. (1987) Distribution of *Rhopalosiphum padi* (Homoptera: Aphididae) on spring barley plants. *Annals of Applied Biology*, **110**, 1–7.

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