



Short communication

## Within-plant distribution of *Rhopalosiphum padi* on wheat seedlings is affected by induced responses

Ernesto Gianoli

Department of Entomology, Swedish University of Agricultural Sciences, P.O. Box 7044, S-750 07 Uppsala, Sweden; Address for correspondence: Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Casilla 653, Santiago, Chile (E-mail: aletheia@abulafia.ciencias.uchile.cl)

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### Introduction

Cereal aphids have distinct patterns of occupation of plants, both in spatial and temporal terms (Dean, 1974). The preferred feeding site of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), on cereal seedlings is the stem base and lower leaves (Dean, 1974; Leather & Lehti, 1982), and this holds for both field and laboratory observations (Wiktelius, 1987). Previous works discussing this pattern of within-plant distribution have considered factors such as nutritional value of the tissues (Leather & Dixon, 1981; Weibull, 1987; Wiktelius, 1987; Wiktelius et al., 1990) and avoidance of extreme temperatures in the field (Wiktelius, 1987).

Plant quality for herbivorous insects can decrease after feeding, due to induced responses of the plant (reviewed in Karban & Baldwin, 1997). Effects of induced responses on the within-plant distribution of the herbivore have also been reported (Edwards et al., 1991 and references therein). This work presents results suggesting that induced responses of wheat (*Triticum aestivum* L.) seedlings to aphid feeding play a role in shaping the within-plant distribution of *R. padi*. In particular, it compares the constitutive as well as the induced quality for the aphid of the stem (preferred site) and the third leaf (non-preferred site) of a three-leaf seedling.

### Materials and methods

**Organisms.** Experimental seedlings of wheat, *Triticum aestivum* L. cultivar Paleta, were grown from seeds provided by INIA, Chile. Seeds were sown

in 250 ml plastic pots filled with compost. Aphid stock colonies, originated from parthenogenetic females collected in cereal fields in Uppsala, Sweden, were kept on wheat cultivar Drabant in a greenhouse. Aphids used for evaluations of fecundity (see below) were previously synchronised to be of uniform age. These experimental aphids were young adults that had not started reproduction but were chosen from cohorts where a first nymph had appeared in the last 12 h, hence indicating imminent reproduction. All the experiments were performed in greenhouses during the spring-summer time, 1998. Temperature ranged from a minimum of  $15 \pm 2$  °C to a maximum of  $28 \pm 3$  °C. Seedlings at the three-leaf stage were used because this is a growth stage at which early colonisation by *R. padi* takes place in cereal fields (Wiktelius et al., 1990).

**Constitutive quality of the preferred and non-preferred sites.** Before assessing the importance of induced responses, the performance of individual aphids (parthenogenetic females) were compared on the stem and the third (uppermost) leaf, the preferred and non-preferred feeding site, respectively. The 8-d fecundity of a single aptera confined to a clip cage was evaluated. Clip cages were attached to the stem and the third leaf of the same seedlings. A *t*-test for dependent samples was applied ( $N = 12$ ).

**Induced responses and aphid performance on preferred and non preferred sites.** After the evaluation of constitutive quality, the following evaluations of aphid performance utilised alate aphids because this morph is the one that undertakes the selection of the

plant site where the colony will be established (Dixon, 1971). In order to produce induced responses in the stem and the third leaf, 20 apterous aphids were placed on either of these sites four days before the evaluation of aphid performance. At the end of this infestation period aphids were removed using a fine camel brush. The 48-h fecundity of alate aphids placed singly inside a clip cage attached to the plant site was used as a measure of aphid performance ( $N = 12$ ). A preliminary experiment showed a high correlation between 48-h fecundity and 8-d fecundity of alate aphids ( $R^2 = 0.85$ ,  $P < 0.001$ ,  $N = 25$ ), hence giving reliability to the use of 48-h fecundity as a fitness parameter. Aphid performance was evaluated on the stem and on the third leaf of previously infested and uninfested seedlings. Thus, eight experimental groups arose after the combination of two treatments (aphid-infested and uninfested), two infestation sites (stem and third leaf), and two evaluation sites (stem and third leaf). Comparisons between uninfested and infested treatments were performed for each of the four combinations of infestation and evaluation sites. A *t*-test for independent samples was applied in each case. Multiple comparisons among treatments (i.e., the use of a multiple-way ANOVA) were avoided because experiments were performed sequentially rather than simultaneously.

*Induced responses and aphid preference.* After determining the consequences for aphids of feeding on previously infested tissue, the question whether alate aphids are able to discriminate between infested and uninfested seedlings was addressed. A choice test between the third leaf (the leaf which aphids usually land on) of stem-infested and uninfested seedlings was performed. Three aphids were introduced into a plastic box (8 cm × 10 cm × 10 cm) with two holes (8 mm diameter) in its base through each of which one leaf of each treatment was passed. The number of aphids on each leaf was observed 24 h later and a Wilcoxon matched pairs test applied ( $N = 14$ ).

## Results and discussion

*Constitutive quality of the preferred and non-preferred sites.* The performance (8 d fecundity) of individual apterous aphids on the stem and on the third (uppermost) leaf were not significantly different ( $P = 0.788$ , *t*-test for dependent samples). Mean ± SE were: stem  $15.71 \pm 1.44$ ; leaf  $15.21 \pm 0.91$ . Therefore, it seems

Table 1. The fecundity of alate *R. padi* after 48 h on control/infested stem and third leaf of wheat seedlings. Means ± SE shown ( $N = 12$ )

Plant site Infested/Evaluated	Fecundity		P-value <sup>a</sup>
	Control	Infested	
Stem/Stem	5.38 ± 0.55	4.79 ± 0.35	0.381
Stem/Leaf	7.34 ± 0.82	4.81 ± 0.53	0.012
Leaf/Stem	5.27 ± 0.48	5.09 ± 0.41	0.744
Leaf/Leaf	5.67 ± 0.49	3.92 ± 0.26	0.005

<sup>a</sup>*t*-test for independent samples.

that the nutritional quality of the preferred site (stem) does not totally account for the pattern of preference of the aphid.

This result somewhat contradicts previous work suggesting a direct relationship between preferred feeding sites and either performance of *R. padi* (Leather & Dixon, 1981) or nutritional content of the tissue (Wiktelius, 1987). However, there are experimental differences between these reports and the present work. On one hand, comparisons between aphid performance on the stem and on upper leaves were made using earing plants (wheat, oat, barley) (Leather & Dixon, 1981), the plant growth stage at which *R. padi* populations usually start to decline (Wiktelius et al., 1990). The present work used early seedlings, the plant growth stage at which aphid colonisation (and first choice of feeding site) usually takes place (Wiktelius et al., 1990). On the other hand, Wiktelius (1987) analysed and compared the soluble nitrogen concentration (mg N/g of fresh tissue) of the stem (10.5) and the leaves (11.4) of tillering plants (barley), but firm conclusions cannot be drawn because of the statistical sample size ( $N = 1$ , pooled samples). Moreover, total nitrogen is not the most meaningful measure of plant quality for aphids because it includes both essential and non-essential amino acids (see Weibull, 1987), as well as N-based secondary metabolites.

It should be kept in mind, however, that differences in patterns of suitability of plant sites for aphid development can be found among cereal species and even among cultivars (Leather & Dixon, 1981 and references therein). Therefore, comparisons across species should be performed with caution.

*Induced responses and aphid performance on preferred and non-preferred sites.* Results are shown in Table 1. Aphid feeding on the stem triggered an in-

duced response that reduced aphid fecundity on the third leaf, whereas no effect on aphid fecundity on the stem was observed. In contrast, aphid feeding on the third leaf produced a local induced response that reduced aphid fecundity on this leaf, but did not affect aphid fecundity on the stem.

It has been reported that *R. padi* infestation on the first leaf of wheat seedlings triggers the induction of defensive chemicals (Gianoli & Niemeyer, 1997a). Moreover, work on *R. padi* infestation on seedlings of a wild wheat showed that the induction of defensive chemicals varied significantly according to the tissue infested (Gianoli & Niemeyer, 1998), and that the induced chemical responses observed in infested leaves was a consequence of translocation of defensive chemicals from the stem (Gianoli & Niemeyer, 1997b). This does not necessarily mean that the pattern of induced responses observed in the present work is a consequence of phytochemical induction. Nonetheless, the two sources of evidence (aphid performance, phytochemistry) converge in the differential responsiveness of the stem and the leaves of wheat seedlings to aphid infestation.

*Induced responses and aphid preference.* Alate aphids showed no preference ( $P = 0.088$ , Wilcoxon matched pairs test) for the third leaf of either uninfested or stem-infested plants. Number of aphids settled  $\pm$  SE was  $0.85 \pm 0.21$  and  $1.50 \pm 0.21$  for uninfested and infested plants, respectively. Since aphid performance was lower on infested leaves (see above) this behaviour seems to be non adaptive. This inability to discriminate for the most suitable resource among plants is somehow surprising given that, at the end, the within-plant choice aphids make (i.e., establishing the colony mainly on stems) is an adaptive one, considering the involvement of induced responses. A similar mismatch between preference and performance among plants has been observed before in *R. padi* (Weibull, 1987, 1990; Pettersson et al., 1996).

The results of this work suggest that selection by *R. padi* of the stem of cereal seedlings as its main feeding site could not be due to its nutritional value but rather to the avoidance of induced responses, which would occur if aphids fed on upper leaves. Further research on the duration and spatial extension of these induced responses, and a deeper characterisation of their effects on aphid performance, is needed before ascribing induced responses a major role in the within-plant distribution of *R. padi* on cereal seedlings. Furthermore, other ecological factors

that aphids are likely to face in the field must also be evaluated in terms of the relative advantage of establishing the colony on the stem instead of on the upper leaves. For instance, the feeding behaviour of polyphagous predators, which are present in cereal fields when plants are at the seedling stage (Chiverton, 1986), should be addressed. Recent work on other systems shows that aphid distribution within the plant may be affected by plant quality (Jackson & Dixon, 1996), natural enemies (Hopkins & Dixon, 1997), or the interaction of both (W. L. Gonz ales, E. Gianoli & H. M. Niemeyer, unpubl.).

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