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Role of hydroxamic acids in the resistance of wheat to the Russian Wheat Aphid, *Diuraphis noxia* (Mordvilko) (Hom., Aphididae)

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Abstract: Wheats and triticales resistant to Russian wheat aphid (RWA), *Diuraphis noxia*, contained medium to very high concentrations of hydroxamic acids. Feeding behaviour and performance of RWA in wheat seedlings differing in hydroxamic acid (Hx) levels, were determined by electrical penetration graphs, and mean relative growth rates, respectively. Higher Hx levels in the seedlings produced a delay in attaining a sustained phloem ingestion, and tended to produce lower mean relative growth rates. These facts support Hx as resistance factors in wheat towards RWA.

1 Introduction

The Russian wheat aphid (RWA), *Diuraphis noxia*, is a species native to the Black Sea region of Eurasia that has recently spread into and caused considerable damage in wheat-growing areas of North and South America. RWA feeds within the whorl of wheat plants, and causes a rolling of the plant's leaves around the aphid colony, thus gaining protection against most natural enemies and also against contact insecticides. Hence, host plant resistance represents a method by which RWA may be economically controlled.

Major efforts to find sources for resistance to RWA in wheat have been undertaken. Most of the sources found originate from areas in the world where RWA is endemic (DU TOIT and VAN NIEKERK, 1985; DU TOIT, 1987, 1988; NKONGOLO et al., 1989; HARVEY and MARTIN, 1990; SOUZA et al., 1991). Resistant lines of triticale and of other Gramineae related to wheat have also been identified (FRANK et al., 1989; WEBSTER, 1990; WEBSTER et al., 1991). Resistance has also been described in hybrids between wheat and wild Gramineae, thus showing promise for transferring genes from wild relatives to wheat (NKONGOLO et al., 1990a). The resistance has been related in some cases to antibiosis, antixenosis or tolerance (DU TOIT, 1987, 1989; WEBSTER, 1990; SCOTT et al., 1991; ROBINSON et al., 1991). However, the biochemical origin of resistance has not been elucidated.

Plants frequently produce secondary metabolites which play a key role in the defence of the plant against pests and diseases (HARBORNE, 1988). Knowledge about the involvement of plant secondary chemicals in the interaction of RWA and wheat may provide a way for increasing plant resistance through the manipulation, by breeding or genetic engineering, of their concentrations in the plant, and also a rapid chemical test for resistance.

Hydroxamic acids (Hx) are one of the most documented cases of mesophyll and phloem constituents of wheat involved in resistance against several species of cereal aphids (NIEMEYER, 1988). They decrease aphid survival and reproduction (ARGANDOÑA et al., 1980; BOHIDAR et al., 1986; THACKRAY et al., 1990), and are also feeding deterrents (NICOL et al., 1992; GIVOVICH and NIEMEYER, 1991, 1994, 1995). In this paper, we report experiments designed to test whether hydroxamic acids are also involved in the resistance of wheat to RWA.

2 Materials and methods

Individuals of *D. noxia* were collected in wheat fields near Santiago, and reared on oat seedlings (*Avena sativa* L. cv. Nahuén, a cereal lacking Hx) in a chamber at 22°C and 6°C range, and L16:D8 photo regime.

For aphid behaviour and performance studies, three wheat (*Triticum aestivum* L.) cultivars (Millaleu, Nobo and Maitén) were selected to represent low, medium and high concentrations of Hx (0.59, 2.4 and 3.4 mmol/kg fr. wt, respectively). Seeds were obtained from Instituto de Investigaciones Agropecuarias (INIA). Seedlings at decimal growth stage 11 (ZADOKS et al., 1974) were analysed for hydroxamic acids, as described (NIEMEYER et al., 1989).

Electrical penetration graphs (EPGs) (TJALLINGII, 1990; VAN HELDEN and TJALLINGII, 1993) were used to follow feeding behaviour to determine the time individual aphids require to start a sustained phloem ingestion (typical phloem waveforms longer than 8 min) and the total duration of sustained phloem ingestion on each of the wheat cultivars studied. Ten individual aphids on each wheat cultivar were monitored. Experiments lasted 12 h. Means of parameters determined were compared among cultivars by Duncan's multiple range test.

Mean relative growth rates (MRGR) were employed to evaluate the performance of individual aphids on each of the wheat cultivars studied. Twelve first or second instar aphid nymphs were weighed and those with similar weights (30–48 μg) were caged individually on the abaxial leaf surface of a test plant, and removed 96 h later for weighing. MRGRs [1/4 (ln final wt in μg – ln initial wt in μg)] were compared among wheat cultivars using Duncan's multiple range test.

3 Results and discussion

The table shows the results from feeding behaviour and performance experiments. As the hydroxamic acid con-

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Table *Feeding behaviour and performance of* D. noxia *in wheat cultivars differing in hydroxamic acid concentrations*

	Wheat cultivars Millaleu low Hx	Nobo medium Hx	Maitén high Hx
Time to reach the phloem (min)	64a	119b	167c
Aphids reaching the phloem (%)	100	70	60
Time in the phloem (min)	161a	213a	201a
MRGR (μg/μg/day)	0.286a	0.235b	0.246b

Numbers in a row followed by the same letter do not differ significantly ($P > 0.05$).

centration in wheat cultivars increased, the proportion of aphids attaining a prolonged phloem phase within the time of the experiment decreased and the time the aphids needed to attain such sustained phloem ingestion increased. This points to Hx as non-phloem feeding deterrents in wheat seedlings.

The duration of sustained phloem ingestion periods did not vary with the Hx levels in the wheat cultivars studied (table). Similar results previously reported for other aphid species feeding on wheat cultivars differing in Hx levels suggest that Hx concentrations in the phloem are below the threshold for deterrency, or that other phloem constituents may mask the deterrent effect (Givovich and Niemeyer, 1991, 1994, 1995).

Mean relative growth rates showed a tendency to decrease, albeit not statistically significant, when aphids fed on plants with higher Hx concentrations. Aphids on a wheat seedling with high Hx levels spent more time searching for a suitable phloem vessel, fed less, ingested less nutrients and hence gained less weight, than aphids in a low Hx seedling. In addition, the decrease in MRGR's may be attributed to the effect of Hx on enzymic systems (Perez and Niemeyer, 1985; Cuevas et al., 1990) leading to a decreased utilization of ingested food or to other effects altering performance (Cuevas et al., 1993).

Interestingly, high levels of resistance to RWA has been found in maize (Webster et al., 1987) and in rye (Nkongolo et al., 1989, 1990b), two cereals that generally contain high levels of hydroxamic acids (Argandoña et al., 1980; Niemeyer et al., 1989).

Hx have been found in wild *Hordeum* species (Barria et al., 1992) and in other wild Gramineae (Niemeyer et al., 1992). In *Hordeum* species, Hx levels correlated inversily with performance of the aphid *Rhopalosiphum padi* (Barria et al., 1992). The exploration of a possible relationship between the varying resistance to RWA found in *Hordeum* species (Clement and Lester, 1990; Kindler and Springer, 1991; Robinson et al., 1991) and in other wild Gramineae (Kindler et al., 1991; Armstrong et al., 1991), and their Hx content should be explored.

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