Variability in Grain Aphid (Homoptera: Aphididae) Performance and Aphid-Induced Phytochemical Responses in Wheat

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ABSTRACT Aphid genotype has been shown to be a source of variability in the induction of phytochemical responses in wheat after aphid infestation as well as in their performance on wheat lines. Two clones of the aphid *Sitobion avenae* (F.) that differed markedly in their ability to thrive in wheat, *Triticum aestivum* L., lines were used to evaluate aphid performance and the phytochemical responses induced by aphid infestation on cultivated and wild wheat. Results showed that differences in aphid performance were not related to processes that trigger phytochemical induction. The magnitude of the induction was not affected by either aphid genotype or wheat line for both wild and cultivated wheat. However, the experiments on cultivated wheat showed a significant statistical interaction of effects (aphid genotype, wheat line) with regard to the magnitude of induction. Because the results from particular aphid–plant genotype combinations could not be extrapolated to other combinations, it is suggested that studies aiming at the characterization of induced responses as plant resistance tools must include not only topics such as aphid genotype and aphid feeding behavior, but also their particular interactions with host–plant genotype. This work cautions about generalizing the outcomes of insect–plant relationships studies.

KEY WORDS *Sitobion avenae*, *Triticum aestivum*, *Triticum urartu*, aphids, induced responses, hydroxamic acids

CONSIDERABLE EVIDENCE SHOWS that damage to plant tissues by herbivores may induce biochemical changes in the plant (cf., Tallamy and Raupp 1991). These induced responses can be affected by plant features such as genotype, ontogeny, and phenology (Coleman and Jones 1991) as well as by herbivores genotype, life history, behavior, and others (Faeth 1991), and by the environmental conditions under which the herbivore–plant interaction occurs (Gianoli and Niemeyer 1996).

Wheat plants show changes in their secondary metabolism after aphid infestation (Leszczynski 1985, Leszczynski and Dixon 1990), which may affect negatively aphid performance (Thackray et al. 1988). Aphid genotype may be a source of variation in aphid-induced phytochemical responses in wheat (Dorschner et al. 1987, Anderson and Peters 1994) and hence modify the effect of such induced responses on insect performance.

The cereal aphid *Sitobion avenae* (F.) is one of the main aphid pests of winter wheat throughout western Europe (Schepers 1989). Sources of resistance to *S. avenae* have been found in some wild *Triticum* species (Di Pietro et al. 1993). Clonal variability in the performance of *S. avenae* on resistant and susceptible wheat lines have been described (Caillaud et al. 1995).

In the current work, 2 clones of *S. avenae* that differed markedly in their ability to thrive in wheat lines (Caillaud et al. 1995) were used to evaluate aphid performance and the phytochemical responses induced by aphid infestation on 2 cultivated, hexaploid wheat cultivars and 2 wild, diploid wheat lines. We measured induced levels of hydroxamic acids (Hx), plant secondary metabolites associated with aphid resistance of cereals (Niemeyer 1988), that are known to increase upon aphid infestation (Niemeyer et al. 1989). The objective of these experiments was to establish whether the clonal differences in aphid performance were correlated with the levels of Hx that were induced in plants after their infestation. The effect of different constitutive levels of Hx was evaluated using 2 lines of wild wheat with low constitutive Hx levels and 2 wheat cultivars with high constitutive Hx levels.

Materials and Methods

Aphids. Clones Sa1 and Sar2 were collected originally from wheat in the Rennes basin in

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Table 1. Values of r_m and Hx induction indexes, INDX (INDX = [Hx] of infested plant/mean [Hx] of control plants) in infested plants of *T. urartu* lines for *S. avenae* clones Sa1 and Sar2

Clone	r_m (mean ± SE)		INDX (mean ± SE)	
	Tu 772	Tu 782	Tu 772	Tu 782
Sa1	0.261 ± 0.009a	0.248 ± 0.011a	1.60 ± 0.44a	1.48 ± 0.69a
Sar2	0.216 ± 0.009b	0.182 ± 0.007b	1.48 ± 0.26a	1.20 ± 0.25a

Means followed by different letters within each 2 clones * 2 plants group are significantly different (Student–Newman–Keuls test).

1990 and 1987, respectively. Stock clones were kept on the favorable hexaploid wheat cultivar Arminda (Caillaud et al. 1995) at 20 ± 1°C and a photoperiod of 16:8 (L:D) h. All the experiments described below were carried out under these environmental conditions.

Plants. Seeds of hexaploid *Triticum aestivum* L. 'Kona' and 'Antilhue' were provided by INIA at Santiago (Chile) and seeds of diploid *Triticum urartu* (Tum.) lines 772 and 782 were provided by the INRA Plant Breeding Station at Le Rheu (France). Stock cultures were kept under environmental conditions described above. Experimental plants were grown individually in plastic tubes in vermiculite.

Infestation and Analysis. Twenty 2nd-instar apterae were confined in a clip cage attached to the primary leaf of a seedling at growth stage 12 (Zadoks et al. 1974). Empty clip cages were placed on control plants. Each treatment included 8 seedlings. After 48 h, aphids were removed and the tissue enclosed in the clip cage was processed for quantification of total Hx as previously described (Niemeyer et al. 1989).

Measurement of Aphid Performance. Five newborn larvae were placed on plants at growth stage 12 (10 replicates for each aphid-plant combination). Their fecundity was recorded daily for 8 d and the intrinsic rate of natural increase (r_m) was calculated using the formula developed by Wyatt and White (1977) as described in Caillaud et al. (1995).

Data from wild wheats and cultivated wheats were analyzed separately by 2-way analysis of variance (ANOVA) with clone and plant as fixed effects. A Student–Newman–Keuls test was used for the comparison of means. For the analysis of induction of Hx an induction index defined as INDX = [Hx] of infested plant/mean [Hx] of control plants was determined for each clone–plant pair. Indexes were square-root transformed to achieve homogeneity of variances.

Results and Discussion

As previously found for a number of wheat lines (Caillaud et al. 1995), r_m values for clone Sa1 were significantly higher than those for Sar2 in both *T. urartu* lines, the line Tu782 being slightly less suitable for aphid performance than Tu772 (Table 1) ($P < 0.001$ for clone effect, $P < 0.05$ for wheat line effect, and $P > 0.33$ for interaction of factors, 2-way ANOVA). However, no differences in the magnitude of induction (INDX) within lines were obtained after infestation by Sa1 and Sar2 (Table 1) ($P > 0.67$ for clone effect, $P > 0.65$ for wheat line effect and $P > 0.86$ for interaction of factors, 2-way ANOVA). These results show that differences in aphid performance are not related to processes that trigger the induction of Hx in these *T. urartu* lines. In addition, constitutive levels of both lines were similar (0.039 ± 0.008 and 0.026 ± 0.007, mean ± SE for lines Tu772 and Tu782, respectively) and nonsignificantly different ($P > 0.59$, 1-way ANOVA). Thus, there was a lack of correlation between aphid performance and Hx levels both before and after aphid infestation. This could be explained by the low levels of Hx in *T. urartu* lines, which are well below the ranges known to affect the performance of *S. avenae* (Bohidar et al. 1986, Thackray et al. 1990). Alternatively, a mechanism other than Hx explaining the aphid–plant interaction may be involved to explain the observed differences in aphid performance. Such a mechanism could be related to the phloem sealing system of the wild wheat lines studied, as suggested by studies of phloem sap collection by stylectomy in resistant and susceptible *T. monococcum* lines and *T. aestivum* cultivars (Caillaud and Niemeyer 1996).

Values of r_m of Sa1 were also higher than those of Sar2 for both cultivated wheat cultivars (Table 2) ($P < 0.001$ for clone effect, $P > 0.39$ for wheat line effect, and $P > 0.33$ for interaction of fac-

Table 2. Values of r_m and Hx induction indexes, INDX (INDX = [Hx] of infested plant/mean [Hx] of control plants) in infested plants of *T. aestivum* cultivars for *S. avenae* clones Sa1 and Sar2

Clone	r_m (mean ± SE)		INDX (mean ± SE)	
	Antilhue	Kona	Antilhue	Kona
Sa1	0.256 ± 0.013ab	0.265 ± 0.021a	1.16 ± 0.14b	1.59 ± 0.10a
Sar2	0.210 ± 0.032c	0.230 ± 0.022bc	1.39 ± 0.22ab	1.01 ± 0.20b

Means followed by different letters within each 2 clones * 2 plants group are significantly different (Student–Newman–Keuls test).

tors, 2-way ANOVA). Because, as was the case for wild wheat, constitutive levels of both cultivars were similar (0.311 ± 0.021 and 0.361 ± 0.018, mean ± SE for cultivars Antilhue and Kona, respectively) and nonsignificantly different ($P > 0.57$, 1-way ANOVA), it was concluded that Hx do not affect the performance of *S. avenae* under these experimental conditions. With regard to the magnitude of Hx induction, no significant effect of aphid clone nor wheat cultivar was found; however, the interaction of factors turned out to be statistically significant ($P > 0.87$ for clone effect, $P > 0.31$ for wheat cultivar effect, and $P < 0.03$ for interaction of factors, 2-way ANOVA). This appeared as a consequence of the fact that induction indices in Kona after infestation by clone Sa1 were significantly higher than with clone Sar2 although no significant interclonal differences were found in cultivar Antilhue (Table 2). These results, together with those from wild wheats, suggest an interaction between plant genotype and aphid clone feeding behavior i.e., particular aphid-plant genotypes combinations may lead to results not predictable from results of other combinations. Therefore, caution should be exercised in determining the generality of mechanisms of induced defenses.

Interestingly, despite inducing higher levels of Hx in plants (Kona), Sa1 showed a better performance than Sar2. Again, at first glance this suggests the involvement of a mechanism of resistance other than Hx. However, this result may be the result of an Hx-avoidance feeding behavior prevailing in this clone–plant genotype interaction, similar to that found in the cereal aphid *Rhopalosiphum maidis* (Fitch) feeding in wheat (Givovich and Niemeyer 1995). In that report, the insensitivity of *R. maidis* to the feeding deterrent properties of Hx was suggested to be caused by a feeding strategy characterized by a low number of cellular punctures in live tissues other than sieve elements during its way to the phloem thus avoiding contact with Hx. Although Givovich and Niemeyer found that Chilean individuals of *S. avenae* did not show such feeding behavior and hence were sensitive to Hx, the possibility that the French clones of *S. avenae* used in this work possessed such a trait cannot be ruled out. An adequate experimental approach (evaluation of feeding behavior) would elucidate this point.

In this work, no clear correspondence was found between aphid performance and Hx levels in plants after infestation both on wild and cultivated wheats. In addition, constitutive levels of Hx in wheat plants did not show a clear-cut effect on such aphid–plant interactions. The current work suggests that studies aimed at the characterization of induced responses as plant resistance tools must include not only topics such as aphid genotype and aphid feeding behavior but also their particular interactions with host–plant genotype because particular aphid-plant genotype combinations may lead to results not predictable from results of other combinations. Thus, this work poses a word of caution in the generalization of outcomes of insect–plant relationships studies.

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