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No risk, no gain? Limited benefits of a non-costly herbivory-induced defense in wheat[1]

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Abstract: Following a short-term infestation by aphids, wheat seedlings show an increase in their concentration of hydroxamic acids (Hx), secondary metabolites conferring resistance against insects. The benefits for a wheat cultivar of Hx induction after aphid infestation were addressed. Benefits were evaluated in terms of *i)* the negative effect upon aphid performance, and *ii)* the enhancement of the competitive status of an inducible cultivar compared with a non-inducible one, in the presence of aphids. A slight effect of Hx induction on early aphid settlement was observed, although it was not statistically significant. Likewise, non-significant differences were found in time to first reproduction, fecundity, adult weight, nymph survival, and intrinsic rate of population increase (r_m), between control and previously infested plants. Therefore, no effect of Hx induction on aphid performance was detected. Issues on the magnitude of the induction as well as on its duration are raised in order to discuss these results. On the other hand, competitive ability of the inducible cultivar was shown to be slightly but significantly improved in the presence of aphids. The mechanism underlying this competitive advantage was not determined. Finally, the ecological significance of the limited benefits of this induced defense is discussed.
Keywords: hydroxamic acids, induced defenses, aphids, wheat, *Triticum*.

Résumé: Après une brève infestation par des pucerons, des plantules de blé ont montré une augmentation de leur concentration en acide hydroxamique (Hx), un métabolite secondaire induisant une résistance contre les insectes. Les avantages de l'induction de Hx après l'infestation par des pucerons sur un cultivar de blé ont été évalués par *i)* l'effet négatif sur la performance des pucerons et *ii)* l'amélioration du statut compétitif d'un cultivar à résistance induite comparé à un cultivar à résistance non induite, en présence de pucerons. Un léger effet de l'induction des Hx a été observé bien que non significatif. Des différences non significatives ont été trouvées au moment de la première reproduction, de la fécondité, du poids de l'adulte, de la survie des nymphes et du taux intrinsèque d'augmentation de la population (r_m) entre les plantes témoin et celles préalablement infestées. Donc, aucun effet d'induction par des pucerons n'a été trouvé. Les résultats sont discutés en rapport avec la durée de l'induction. D'un autre côté, la qualité compétitive du cultivar à résistance induite a été améliorée légèrement mais significativement avec la présence des pucerons. Le mécanisme à l'origine de cet avantage compétitif n'a pas été determiné. Enfin, on discute la signification écologique de quelques avantages procurés par la défense induite.
Mots-clés: acides hydroxamiques, défenses induites, pucerons, blé, *Triticum*.

Introduction

Phytochemical responses induced by feeding of herbivorous insects have been reported for a wide variety of systems (Tallamy & Raupp, 1991; Karban & Baldwin, 1997). A common shortcoming in these studies as discussed by Fowler & Lawton (1985) is the lack of reliable data on the ecological significance of such induced responses. Work on induced phytochemical responses only sometimes includes evaluations of their associated costs and benefits to the plant (Baldwin, 1991). Without this, little can be concluded about the actual role of induced responses in plant-insect interactions. Consequently, to achieve an appropriate understanding of the ecological significance of induced responses, it is necessary to address the following issues: *i)* effect of the increased level of secondary metabolites on the fitness of the herbivore; *ii)* costs in terms of plant fitness of the induced defenses; and *iii)* effect of the induction on other ecological processes, *e.g.*, plant competition, insect predation and/or parasitism. In addition, the characterization of the induced responses, and the identification of the biotic as well as abiotic constraints to their expression, would provide useful information to assess more accurately the importance of such phenomena on the probable scenarios in which the plant-insect interaction takes place.

We have been working with a plant-herbivore system involving wild and cultivated wheat (*Triticum uniaristatum* and *T. aestivum,* respectively) and cereal aphids (Aphididae). Following a short-term infestation by aphids, wheat seedlings showed an increase in their concentration of hydroxamic acids (Hx) (Niemeyer *et al.*, 1989), a class of secondary metabolites typical of Poaceae (Gramineae) (Niemeyer, 1988). Constitutive levels of Hx have been shown to deter aphid feeding and decrease aphid survival and reproduction (Argandoña *et al.*, 1980; Thackray *et al.*, 1990; Niemeyer & Pérez, 1995 and references therein). In addition, the constitutive accumulation of Hx did not entail a cost in terms of grain yield and was related to field resistance against aphids in several wheat cultivars (Gianoli, Papp & Niemeyer, 1996). The induction of Hx in wheat by aphid infestation was affected by plant genotype (Niemeyer *et al.*, 1989), environmental conditions (Gianoli & Niemeyer, 1996) and aphid genotype (Gianoli *et al.*, 1997); whereas neither nutrient-supply regime nor leaf ontogeny affected the magnitude of Hx induction (Gianoli & Niemeyer, 1997a). Work on wild wheat showed that the

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induction of Hx was a short-term and localized response (Gianoli & Niemeyer, 1998), and that it does not impose a cost in terms of components of plant fitness (Gianoli & Niemeyer, 1997b).

In this paper we report the further characterization of aphid-induced Hx in wheat and its ecological significance. The possible benefits of Hx induction after aphid infestation for a wheat cultivar are addressed. These benefits are evaluated from two different approaches. First, the negative effect upon aphid performance of induced Hx in seedlings is evaluated in the laboratory. Second, the competitive ability of two cultivars showing the same levels of constitutive Hx but differing in their induced responses is compared in the presence and absence of aphids.

Material and methods

ORGANISMS

Seeds of wheat, *Triticum aestivum* L. cultivars were obtained from INIA, Chile and Campex-Baer, Chile. They were germinated in individual plastic pots (25 ml) filled with potting soil. Seedlings developed in a growth chamber at 20°C and L12:D12 photoperiod, and were watered every two days with tap water.

Stock colonies of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.) were maintained on oat plants (an Hx-lacking cereal) in a room at 20 ± 1°C and L12:D12 photoperiod. Under these conditions aphid reproduction is parthenogenetic.

EVALUATION OF HX INDUCTION

A protocol devised to evaluate induction of Hx by aphids was applied to two wheat cultivars (Cisne and Millaleu) which had shown similar levels of constitutive Hx but differed in the levels of Hx attained after aphid infestation in preliminary trials (Gianoli, unpubl. data). These trials were done under the same conditions as those in this work. Experiments were performed in the growth chamber as described above. When wheat seedlings attained growth stage 12 (primary leaf fully unfolded, secondary leaf visible, Zadoks, Chang & Konsak, 1974), each one was infested with 20 individuals of *R. padi* (second or third instar apterae) confined in a clip-cage (2 cm diameter × 2 cm height) attached to the primary leaf. Empty clip-cages were placed on control plants. Treatments were assigned randomly (8 replicates per treatment). After 48 hours of infestation, clip-cages were removed and aphids were withdrawn from the infested seedlings with a fine brush. Immediately after aphid removal, primary leaves of both control and treated plants were analyzed for DIMBOA, the main Hx aglucone in wheat extracts (Niemeyer, 1988), by HPLC as previously described (Gianoli & Niemeyer, 1997c).

EFFECT OF HX INDUCTION ON APHID PERFORMANCE

The rationale of this experiment was that, following aphid infestation, only the inducible cultivar (Millaleu) would show a difference in aphid performance in comparison with control plants due to the Hx increase. For cultivars Cisne and Millaleu, parameters of aphid performance were measured in control and infested seedlings immediately after the end of the infestation period (48 hours) described above. Three adult *R. padi* randomly selected from the stock culture were placed in a clip cage attached to the primary leaf and cages were observed continuously. The time (hours) to the first reproduction of these adult aphids was evaluated. Adult aphids were then removed and the time (days) to the first reproduction D, of the new born nymph was recorded. Then its fecundity M, was recorded during D days, the adult being removed and weighed at that time. Finally, survival of the produced nymphs was evaluated. The r_m value was calculated as: $r_m = 0.74 (\ln M) / D$, following Wyatt & White (1977). Experiments were replicated 10 times and were performed in the growth chamber described above.

COMPETITION BETWEEN WHEAT CULTIVARS

This experiment was performed outdoors, in gardens of the campus of the Faculty of Sciences, University of Chile. Conditions were as follows (spring time): 14 hours daylength, temperature minimun 10-14°C, maximum 24-30°C. The two wheat cultivars utilized for the previous experiment (Cisne, non-inducible, and Millaleu, inducible) were evaluated for competitive ability in the presence and absence of aphids. Seeds of both cultivars were sown in plastic pots (2.5-L) filled with soil (Anasac) in monoculture and in 50% mixtures. Twenty-four seeds were sown in each pot. Each pot was isolated by a cylindrical cage made of transparent acetate with a fine mesh screen at the top. Identification of plants in mixtures was achieved by using a planting grid. Data for each cultivar in mixed pots were treated independently. Thus, 8 groups arose from the combination of two cultivars (Cisne and Millaleu), two seed ratios (50% and 100%), and two treatments (infested and non-infested). Each group was replicated three times. Another set of pots was artificially infested with aphids. Two weeks after sowing 100 adult *R. padi* (10 alatae and 90 apterae) were dropped in each of these pots. One week later the infestation was repeated. Four weeks after sowing the experiment ended and all plants were harvested. Fresh weight of the shoot and number of leaves were recorded for each single plant and averaged for each pot. Data were analyzed by a three-way ANOVA with Ratio, Cultivar and Aphids as main effects and LSD tests were performed for planned comparisons. In addition, following Windle & Franz (1979), we assessed the comparative aggressiveness of cultivars Cisne (C) and Millaleu (M) by calculating the relative crowding coefficient (K):

$$K_{CM} = \frac{W_C mix}{W_M mix} \times \frac{S_M mix}{S_C mix} \times \frac{W_M mon}{W_C mon} \qquad [1]$$

where W is biomass, S is number of seeds, *mix* is mixture, and *mon* is monoculture. Higher K values indicate more aggressiveness.

Results

EVALUATION OF HX INDUCTION

As found in preliminary trials, cultivars Millaleu and Cisne showed very similar constitutive levels of Hx, but differed in their capacity to increase Hx levels following aphid infestation, cultivar Millaleu being the inducible one.

Thus, this proved to be a suitable system for experiments addressing the benefits of Hx induction. Mean ± SE of Hx (mmol/kg fresh weight) in cultivar Cisne were 0.73 ± 0.15 and 0.73 ± 0.13 for control and infested plants, respectively ($P > 0.99$, one-way ANOVA). Cultivar Millaleu showed values of 0.71 ± 0.03 and 0.84 ± 0.05 for control and infested plants, respectively ($P < 0.03$, one-way ANOVA).

EFFECT OF HX INDUCTION ON APHID PERFORMANCE

Parameters related to aphid performance were evaluated sequentially, thus allowing us to determine the time-span of the hypothetical effect of Hx induction. The first parameter, time to the first reproduction, was similar for aphid on control and infested Cisne plants (Figure 1a). Differences in the frequency distribution of time to the first reproduction were evaluated by a Kolmogorov-Smirnov two-sample test. Aphids on infested Millaleu plants (the cultivar showing Hx induction) tended to reproduce later than on control plants (Figure 1b), however, the difference was not statistically significant ($P > 0.05$), probably due to the small sample size. Likewise, non-significant differences ($P > 0.05$, one-way ANOVA) were found in time to first reproduction of newly born nymphs, total fecundity, adult weight, survival of produced nymphs, and intrinsic rate of population increase (r_m) of aphids on control and infested treatments of both cultivars (Table I). Therefore, no effect of Hx induction on aphid performance was detected in the inducible cultivar Millaleu.

COMPETITION BETWEEN WHEAT CULTIVARS

Aboveground biomass (mg) was different among the six pot-treatments which comprised the 8 experimental groups after an initial one-way ANOVA: $F = 5.93$, $P = 0.01$. However, after including "number of plants per pot" as a covariate in the analysis, the effect of post-treatment was no longer significant: $F = 0.25$, $P = 0.93$. Therefore, pot-treatments were comparable in terms of mean plant biomass. This result also pointed out that germination rates were different for the wheat cultivars evaluated; in fact,

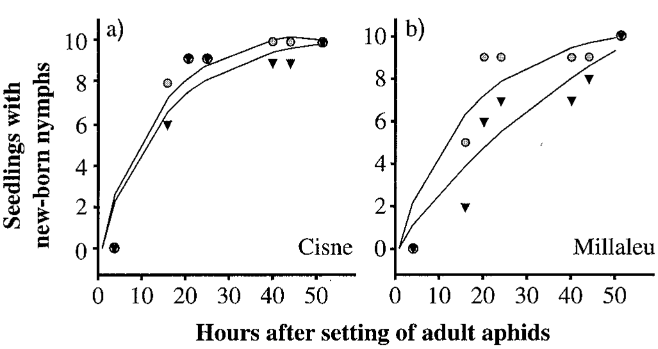

FIGURE 1. Time to first reproduction of adult aphids transferred to wheat seedlings immediately after a controlled aphid infestation. Points represent the cumulative number of seedlings ($n = 10$) with new-born nymphs through time. Evaluations were performed in control (○) and infested (▼) seedlings of cultivars Cisne (a) and Millaleu (b). Concentration of hydroxamic acids in Millaleu was inducible after aphid infestation, that of Cisne was not. Lines describe the fit of each plot to the curve $Y = a(1 - e^{-bx})$.

TABLE I. Days to first reproduction (D), fecundity (nymphs produced during D days), intrinsic rate of increase (r_m), nymph survival (%), and final adult weight (μg) of the aphid *Rhopalosiphum padi* in the primary leaf of infested and control wheat seedlings[a] ($n = 10$). Wheat cultivars had similar constitutive levels of hydroxamic acids (Hx) but differed in the ability to show induced levels of Hx following aphid infestation: Cisne (non-inducible) and Millaleu (inducible)

	Cisne Control	Cisne Infested	P^b	Millaleu Control	Millaleu Infested	P^b
D	6.1 (0.3)	6.5 (0.2)	0.40	5.1 (0.3)	5.6 (0.4)	0.41
Fecundity	13.5 (1.8)	11.6 (1.6)	0.50	13.9 (2.1)	17.4 (2.0)	0.32
r_m	0.099 (0.03)	0.059 (0.01)	0.26	0.136 (0.03)	0.159 (0.03)	0.62
Nymph survival	0.78 (0.02)	0.87 (0.04)	0.12	0.80 (0.05)	0.85 (0.04)	0.53
Adult weight	237.6 (25.0)	220.8 (14.9)	0.57	286.0 (17.5)	274.4 (21.9)	0.74

[a]Means (SE).
[b]One-way ANOVA.

Millaleu showed 85% germination and Cisne only 51%. These differences could be ignored by comparing mean plant biomass per pot.

Mean plant biomass (log-transformed to fit ANOVA assumptions) was not significantly affected by Cultivar, Ratio or Aphids or by any of the interactions of these factors (all P-values higher than 0.07, three-way ANOVA). Means are shown in Table II. Nonetheless, planned comparisons of selected means (LSD-test) showed that aphid infestation and hence Hx induction gave the inducible cultivar Millaleu a slight benefit in terms of competition with respect to the non-inducible cultivar Cisne. All comparisons performed and their significance levels are listed in Table III. Furthermore, the mean number of leaves produced per group was not affected either by the factors evaluated (Cultivar, Ratio, Aphids) or by their interaction (all P-values > 0.21, three-way ANOVA). Unlike plant biomass, no difference among groups was observed following the evaluation of planned comparisons (LSD-test, data not shown). Finally, although the relative crowding coefficient (K) was always higher for Cultivar Millaleu ($P < 0.003$, two-way ANOVA), the increase in K in the presence of aphids on Millaleu was not significant ($P > 0.62$, LSD-test). Millaleu values of K (Mean ± SE) were 1.11 ± 0.03 and 1.16 ± 0.09 without and with aphids, respectively. Those of Cisne were 0.89 ± 0.03 and 0.87 ± 0.07 without and with aphids, respectively.

Discussion

The benefit to a plant of a chemical defense is properly evaluated when it is measured in terms of a currency of plant fitness, in the presence of herbivores (Dirzo & Harper, 1982). However, since resistance to herbivory is assumed to benefit plants, other indirect measures such as reduced herbivory (Simms & Rausher, 1987) or detrimental effect on herbivores (Berenbaum, 1978) may also be useful to assess benefits of chemical defenses. The same should hold for induced chemical defenses (Baldwin, 1991; Karban, Agrawal & Mangel, 1997). In addition, it must be pointed out that any measure of benefits of induced defenses expressed in terms of plant fitness necessarily embodies

TABLE II. Mean ± SE shoot weight (mg) of wheat cultivars Cisne (C) and Millaleu (M) at 50% and 100% seed ratios, and under presence/absence of aphids. Plants were 4-weeks old

	Cisne		Millaleu	
Ratio	Aphids absent	Aphids present	Aphids absent	Aphids present
C	18.64 ± 0.14	18.84 ± 0.23		
C:M	17.58 ± 0.41	17.78 ± 1.27	19.66 ± 1.01	20.58 ± 1.90
M			18.66 ± 0.23	19.06 ± 0.80

their associated costs (Wold & Marquis, 1997). In this way, what is actually measured are the net benefits of induced defenses (net benefits = true benefits - cost of induction - cost of damage).

The present study failed to find a significant difference in aphid performance on two wheat cultivars differing in their levels of induced Hx (Table I). These results differ from those of Thackray, Morse & Leech (1988) in a similar aphid-wheat-Hx system, where reduced growth rate of cereal aphids on previously infested plants was reported. An explanation to this apparent contradiction could lie in the variability for the trait "Hx induction" observed in wheat cultivars (Niemeyer *et al.*, 1989), as well as in a probable effect of aphid genotype on the outcome of the interaction (Gianoli *et al.*, 1997). In short, the particular aphid species (and even aphid clone) and wheat cultivar involved in the interaction can influence the degree to which Hx are induced.

The increase of Hx in infested seedlings of cultivar Millaleu did not affect aphids in a detectable way, in spite of earlier experimental evidence of an inverse relationship between Hx levels and aphid performance (Argandoña *et al.*, 1980; Bohidar Wratten & Niemeyer, 1986; Thackray *et al.*, 1990; Givovich & Niemeyer, 1995). Two main points could account for this apparent inconsistency. First, assuming that induced levels of Hx were not relaxed during the performance evaluations, the magnitude of the difference between constitutive and induced levels (0.13 mmol/kg fresh weight, 18% of increase) is about 20 times smaller than the range of Hx concentrations used in characterizing the inverse relationship between Hx and aphid performance. Thus, Hx induction in Millaleu could be too small to generate a negative effect of Hx upon aphids. Second, and now assuming that the magnitude of Hx induction is not negligible, work on a wild *Triticum* species has shown that the induction of Hx by aphid infestation relaxed after 48 hours (Gianoli & Niemeyer, 1998). Thus, not overlooking possible differences due to plant genotype, this result suggests that a similar scenario could have occurred in the present work, *i.e.*, aphids being exposed solely to a short-term increase of Hx, leading to the lack of effect on the parameters of aphid performance evaluated. Interestingly, the only difference that suggested the existence of such an effect was found for the first parameter evaluated in time: time to the first reproduction.

Cultivars Milalleu and Cisne showed a close similarity in productivity, *i.e.*, mean plant biomass at the end of the experiment (Table III), providing a suitable system to evaluate benefits of Hx induction for a wheat cultivar in terms of enhanced plant fitness in the presence of herbivores. Competitive ability of cultivar Millaleu was shown to be slightly improved in the presence of aphids, outcompeting cultivar Cisne only under these conditions (Table III). A similar trend, although non-significant, was shown by crowding coefficients (K). The competitive advantage of cultivar Millaleu in the presence of aphids might be viewed as a benefit of Hx induction since this cultivar was inducible and cultivar Cisne was not. However, the fact that aphid performance on Millaleu was generally greater than that on Cisne (Table I) challenges the assertion of a benefit gained by Millaleu owing to Hx induction. Thus, at first sight it would be expected that the competitive advantage of Millaleu over Cisne, observed only in the presence of aphids, was a consequence of hindered aphid population development caused by the induction of Hx. Results of aphid performance evaluations, however, failed to support this hypothesis. Nonetheless, the issue of time of aphid exposure to induced Hx in each experiment could be a confounding factor. Thus, it may be speculated that in the competition experiment, aphids on Millaleu experienced the effects of a prolonged Hx induction triggered by a larger number of aphids on the plant, thereby aphids were more affected than in the performance experiment, where a single stimulus of induction was applied prior to the evaluations. Further experiments assessing the fate of aphids in the competition experiment may shed light upon this speculation.

Alternatively, other factors involving aphids may account for the observed advantage of Millaleu. First, it must be pointed out that growth (final biomass) of both wheat cultivars was unexpectedly not affected by aphid infestation. Therefore a hypothesis of "overcompensation" (Owen & Wiegert, 1976), *i.e.*, enhanced growth of plants

TABLE III. Selected comparisons of means from Table II (LSD-test after three-way ANOVA) and questions thereby answered. Concentration of hydroxamic acids (Hx) in wheat cultivar Cisne was non-inducible after aphid infestation, and that of Millaleu was inducible. Codes: 100M0 = Millaleu at 100%, without aphids; 50C1 = Cisne at 50%, with aphids; 100C0 = Cisne at 100%, without aphids; 50M1 = Millaleu at 50%, with aphids; 50C0 = Cisne at 50%, without aphids; 50M0 = Millaleu at 50%, without aphids; 50C1 = Cisnes at 50%, with aphids; 100C1 = Cisne at 100%, with aphids

Question	Comparison	P-value	Answer
Do cultivars differ intrinsically in productivity?	100C0 *versus* 100M0	0.99	No
Do aphids affect Cisne?	100C0 *versus* 100C1	0.89	No
Do aphids affect Millaleu?	100M0 *versus* 100M1	0.77	No
Does Millaleu surpass Cisne (aphids absent)?	50M0 *versus* 50C0	0.14	No
Does Millaleu surpass Cisne (aphids present)?	50M1 *versus* 50C1	0.05	Yes
Does Millaleu affect growth of Cisne (aphids absent)?	100C0 *versus* 50C0	0.44	No
Does Millaleu affect growth of Cisne (aphids present)?	100C1 *versus* 50C1	0.86	No

after herbivory, to explain the slight competitive advantage of Millaleu may be discarded. Finally, a more complicated hypothesis addresses a type of competition other than competition by exploitation, *i.e.*, competition by interference between wheat cultivars by means of allelopathy. Thus, the set of chemical responses of Millaleu following aphid infestation might encompass the release of allelopathic compounds in root exudates, hence negatively affecting the growth of Cisne. Hx in wheat and rye have been identified in this role previously (Pérez & Ormeño-Núñez, 1991). However, growth of Cisne was not affected by the presence of Millaleu in mixed pots either in the presence or in the absence of aphids (Table III).

Induction of Hx in this system was shown to be non-costly to the plant in terms of fitness parameters (Gianoli & Niemeyer, 1997b). The present work shows limited benefits of such induced defense. In the realm of Optimal Defense theory (McKey, 1974; Rhoades, 1979), patterns of defense allocation in plants are thought to be shaped by minimizing costs and maximizing benefits of the allocations. Although the cost/benefit relationship of a given defense allocation shifts with the ecological scenario the plant is facing (*e.g.*, herbivore abundance, plant competition, habitat quality), our system has been evaluated for costs and benefits under rather similar conditions and hence allows a general statement. A trait such as Hx induction, showing limited costs as well as limited benefits, would have a null selective value, *i.e.*, it would be neutral. Therefore, a prediction cannot be made regarding the role of this trait in future scenarios of plant-insect interactions. It must be stressed that the former discussion assumes that the trait Hx induction is under some degree of genetic control. Although traits of cultivated wheat are mostly a consequence of artificial selection oriented towards agronomic features, it cannot be ruled out that genetic material from wild relatives of wheat has survived breeding programs. An appropriate evaluation of genetic variability for induced Hx should be performed with wild Poaceae, which contain Hx (Niemeyer, Copaja & Barrìa, 1992).

The results of this work suggest that Hx induction has little ecological significance, at least for this particular insect-plant interaction. Thus, no benefit of Hx induction was found in an inducible wheat cultivar with respect to negative effect on aphid performance. Likewise, only a marginally significant effect of Hx induction was detected on the enhancement of the competitive status of the inducible cultivar compared with a non-inducible cultivar. However, the reported sensitivity of Hx induction to both biotic and abiotic factors (see Introduction) allows us to expect rather variable outcomes in its costs and benefits under field conditions. In addition, the coarse mechanism underlying the competitive advantage mentioned above is far from being clear. Further work must address this topic, as well as the temporal scale of Hx induction in relation to its hypothetical effect on aphids.

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