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EFFECT OF DIMBOA, AN APHID RESISTANCE FACTOR IN WHEAT, ON THE APHID PREDATOR *Eriopis connexa* GERMAR (COLEOPTERA: COCCINELLIDAE)

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Abstract—DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one), a secondary metabolite found in cereal extracts, confers resistance in wheat to aphids. Its effect on beneficial organisms was tested on larvae of the aphid predator *Eriopis connexa* Germar. Larvae were fed until pupation on artificial diets to which different concentrations of DIMBOA (2–200 μg/g diet) were added, as well as on aphids that had been feeding on wheat seedlings with different DIMBOA levels (140–440 μg/g fresh tissue). In diets, the effect of DIMBOA was greatest on survival of third-instar larvae and on the duration of the second and fourth instars. When aphids were provided as food, those that had fed on a wheat cultivar with an intermediate DIMBOA level led to a significantly longer larval duration in the predator than did those that fed on either low or high DIMBOA cultivars. Shortest predator development times were obtained with aphid prey that had fed on high DIMBOA seedlings. Higher DIMBOA levels in the plant appear to reduce aphid feeding rates (and rates of DIMBOA ingestion), decreasing aphid survival and minimizing the effect of the toxin on the predator.

Key Words—Wheat, hydroxamic acids, DIMBOA, plant resistance, cereal aphids, Homoptera, Aphididae, aphid predators, *Eriopis connexa*, Coleoptera, Coccinellidae, tritrophic interactions.

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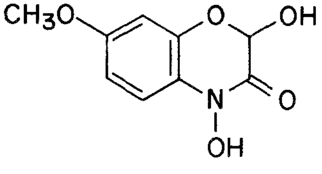
INTRODUCTION

The most prevalent cereal aphids in Chile are *Metopolophium dirhodum* (Walk.), *Sitobion avenae* (Fab.), *Schizaphis graminum* (Rond.), and *Rhopalosiphum padi* (L.) (Ramírez, 1990). Although an array of natural enemies, which includes predators, parasitoids, and pathogens limit their populations to a great extent (Zúñiga, 1987), aphids constitute a potential problem due to their ability to transmit virus diseases, such as the barley yellow dwarf virus (BYDV) (Herrera and Quiroz, 1988). *Eriopis connexa* Germar (Coccinellidae) is one of the most important aphid predators in Chile because of its high populations in spring and summer, wide range of prey, and predatory efficiency (Macfarlane, 1985).

DIMBOA (2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one), the main hydroxamic acid (Hx) present in wheat extracts (Niemeyer, 1988a), has been associated with resistance of the plant to aphids through antibiosis (Argandoña et al., 1980; Bohidar et al., 1986; Thackray et al., 1990; Wratten et al., 1991) and feeding deterrency (Argandoña et al., 1983; Niemeyer et al., 1989b; Givovich and Niemeyer, 1991).

Biological control and host-plant resistance are often compatible and even complementary (Emden and Wratten, 1991), as has been found to be the case of resistance in varieties of barley and sorghum that complemented the activity of the parasitoid *Lysiphlebus testaceipes* Cresson (Starks et al., 1972). However, variations in host plants may have dramatic effects on biological control agents. Thus, prey confined to resistant host plants may represent a low-quality food for predators and parasitoids, affecting their biology (Bergman and Tingey, 1979). Secondary metabolites in the plants may be the cause of detrimental effects on organisms at the third trophic level, as is the case of α-tomatine, an alkaloid in *Solanum* and *Lycopersicon* species, that is toxic to the endoparasitoid *Hyposoter exiguae* (Viereck), which takes up the compound through its host *Heliothis zea* (Boddie) (Campbell and Duffey, 1979). Nicotine, an alkaloid from *Nicotiana* species confers plant resistance to *Manduca sexta* L. but has negative effects on the parasitoids *Hyposoter annulipes* (Cresson) and *Cotesia congregata* (Say) developing on *M. sexta* larvae reared in nicotine-containing diets (Thorpe and Barbosa, 1986; Barbosa et al., 1986). Plant secondary metabolites might



DIMBOA

SCHEME 1.

confer resistance in the herbivore towards the predator, as is the case of *Macrosiphon albifrons*, an aphid that is protected from attack by *Carabus problematicus* by quinolizidine alkaloids ingested from its lupin host plants (Wink and Römer, 1986).

An increase in Hx levels in wheat, proposed as a mechanism to enhance resistance towards aphids (Niemeyer, 1988b; Copaja et al., 1991a,b; Wratten et al., 1991), could affect beneficial organisms. Hence, the effect of DIMBOA on the development of *E. connexa* was examined.

METHODS AND MATERIALS

A mass rearing technique and an artificial diet for *Eriopis connexa* were developed; the direct effect of DIMBOA was studied by adding the compound in different concentrations to the diet; finally, larvae were fed aphids reared on wheat lines containing different DIMBOA levels.

Mass Rearing of E. connexa. Rearing was started with 25 pairs of coccinellids collected in fields near the laboratory. Beetles were fed on the aphid *R. padi* reared on oat seedlings in a room maintained at 21°C with a 10°C range, 50% relative humidity with a 10% range and a 16:8 light–dark photoregime.

All stages of the predator were maintained separately in plastic containers of 12 cm diameter and 7.5 cm height fitted with a cover with fine holes. Adults were confined at a density of five to eight pairs per container. Aphids on oat leaves were placed as food on a sheet of paper towel inside the container. Egg groups were collected daily and maintained separately in containers. Larvae were also fed with aphids from oats; these aphids were offered as soon as egg hatch occurred. The fourth instars were supplied with a sheet of paper towel for pupation. The mean number of aphids provided daily per larva from first to fourth instar were 10, 25, 20, and 15, respectively. Pupae were collected daily and were placed on a sheet of paper towel inside a container. Adults that had emerged within the same 24-hr period were sexed and maintained in pairs in the containers.

Artificial Diet for E. connexa. Diets were based on those developed for coccinellids using liver and meat extracts (Herrera, 1960; Atallah and Newson, 1966; Ferran and Laforge, 1975) and were tested by rearing first-instar larvae in 5.5-cm-diam. Petri dishes, each larva receiving 0.5 g diet every two or four days. Table 1 shows the best formulation of those tested.

Pollen with polyvitamins and wheat germ were pulverized separately with a mortar and pestle. These constituents were mixed with sorbic acid, ascorbic acid, and vitamin E, and then bee honey was added. This mixture was blended for 30 sec with liver in 50 ml water in a domestic blender. Agar was dissolved in 50 ml water at 80°C and cooled down before being mixed into the previous

TABLE 1. COMPOSITION OF ARTIFICIAL DIET FOR *E. connexa*

Component	Quantity (g)
Cooked pig liver	68.1
Pollen	10.0
Honey	10.0
Wheat germ	5.0
Agar	4.0
Polyvitamins	1.0
Sorbic acid	1.0
Ascorbic acid	0.5
Vitamin E	0.4
Water	100.0

mixture for 1 min. The homogeneous dough of semisolid texture obtained was dispensed to sterilized containers and stored at 6°C.

The diet was tested with 10 first-instar larvae and was renewed every two days. For comparison, 14 first-instar larvae were reared individually with natural diet using *R. padi* nymphs ad libitum as food.

Effect of DIMBOA in Artificial Diets on Development of E. connexa. First-instar larvae of *E. connexa* were reared on artificial diet containing DIMBOA, isolated from ethereal extracts of *Zea mays* cv. T129s, as previously described (Queirolo et al., 1983). This compound was incorporated to the diet at the required concentration in 50 ml of water before adding the agar suspension. The latter was cooled down before use in order to minimize decomposition of DIMBOA. Analysis of the diet after four days at room temperature revealed that at least 85% of DIMBOA remained in it. Experiments were carried out in a completely randomized design with six treatments and two replicates. Treatments consisted of five DIMBOA concentrations in artificial diet plus a control without DIMBOA. Concentrations tested were 0, 2, 5, 10, 50, and 200 μg DIMBOA/g diet. Each replicate consisted of 10 recently hatched larvae of *E. connexa* maintained separately in 5.5-cm-diam. Petri dishes. The diet (0.5 g) was renewed every four days for the first and second instars and every two days for the third and fourth instars. The Petri dishes were sealed with Parafilm to keep larvae from escaping and diet from drying. Larval mortality, duration of each instar, pupal mortality, pupal duration, weight of pupae, and time to reach adulthood were evaluated.

Study of E. connexa *Larvae Fed on Aphids Reared on DIMBOA-Containing Wheat Lines.* Three wheat lines with different contents of the compound were chosen (Millaleu: 140 μg DIMBOA/g fresh tissue, Nobo: 270 μg, and Maiten: 440 μg). Oats were used as a control without DIMBOA. Aphids (*R. padi*) were allowed to feed on the plants for 24 hr. They were placed within a clip cage located in the middle third of the leaf of a wheat seedling in the one-leaf stage, the stage at which DIMBOA was analyzed. One first-instar larva of *E. connexa* was placed inside each Petri dish with a piece of wet filter paper and allowed to develop to the adult stage. Aphids were removed from the plants and placed inside the Petri dish ad libitum for the larvae. For each wheat cultivar and the oat control there were 10 replicates. Survival of larvae, number of aphids eaten per larva, and the duration of each larval developmental stage were determined. The larvae employed were obtained from eggs laid by field-collected females that had been kept together with males for two weeks under the rearing conditions described above.

Plant Material and Hydroxamic Acid Analysis. Wheat seedlings used were in the one-leaf stage (G.S. 11) (Zadoks et al., 1974). Hydroxamic acids were analyzed by reverse-phase high-performance liquid chromatography, as previously described (Niemeyer et al., 1989a).

RESULTS

Mass Rearing of E. connexa. This technique was developed in order to obtain uniform individuals in high quantities for laboratory assays. Mating was frequent and occurred from early adulthood up to just before death. Females began oviposition on average 16.5 days after reaching adulthood, and the oviposition frequency was every three to four days. Eggs were laid in groups, usually on the surface of paper towel, each batch comprising about 25 eggs. Individuals older than three months laid a higher proportion of infertile than fertile eggs. Eggs were collected daily by cutting the paper around the batch; they hatched five days later.

Larvae were voracious, consuming on average 54, 39, 55, and 72 nymphs of *R. padi* in first, second, third and fourth instars, respectively. Development times for each stage are given in Table 2. The pupal stage lasted 5.4 days and the sex ratio was 1:1. These adults consumed 15–20 aphids per day. The life cycle was completed in 44 days.

Artificial Diet for E. connexa. The rearing of *E. connexa* under laboratory conditions is relatively easy and cheap with aphids as food. However, experiments in which the effect of a given compound is being investigated demand the use of an artificial diet for rearing. Table 2 shows comparative data on larval and pupal development of *E. connexa* on natural and artificial diets. Larvae were reared on artificial diets from first instar to adulthood. Molting was normal, with no mortality recorded. However, the larval developmental period was different from that observed with natural diet, and adults, although being as large as the controls, were whitish in color, possibly due to a lack of appropriate pigments in the diet.

Effect of DIMBOA in Artificial Diet on Development of E. connexa. Table 3 shows the effect of DIMBOA in an artificial diet on the development and survival of larvae of *E. connexa*. Survival was not significantly affected by DIMBOA, with the exception of that of the third-instar larva. In this case, progressively lower survival was obtained with diets with higher DIMBOA concentrations.

The durations of instars two and four were significantly increased by higher DIMBOA concentrations in the diet, albeit only at the highest concentration in the latter instar.

Table 4 shows the overall effect of DIMBOA on larval development and survival and also the effect on pupae and adults obtained from treated larvae. While an increase in time to reach adulthood seems apparent at the lowest

TABLE 2. COMPARATIVE DEVELOPMENT TIMES FOR LARVAE AND PUPAE OF *Eriopis connexa* IN NATURAL AND ARTIFICIAL DIETS

		Time period (days)								
		Larvae						Larva to adult	Survival (%)	
Diet	N^a	I	II	III	IV	Total	Pupae	Total	Larvae	Pupae
R. padi	14	2.9	2.2	4.3	7.6	17.0	5.4	22.4	100	100
Diet	10	5.4	4.7	5.4	9.0	24.5	5.6	30.1	100	100

[a] Number of individuals studied.

TABLE 3. EFFECT OF DIMBOA ON LARVAE OF *Eriopis connexa* REARED ON ARTIFICIAL DIET[a]

Treatment (μg DIMBOA/ g diet)	Instar 1		Instar 2		Instar 3		Instar 4	
	Duration (days)	Survival (%)	Duration (days)	Survival (%)	Duration (days)	Survival (%)	Duration (days)	Survival (%)
0	6.2 a	95.0 a	7.3 a	95.0 a	7.0 a	94.5 a	8.7 a	83.0 a
2	5.3 a	90.0 a	8.7 ab	89.0 a	9.3 a	81.3 ab	9.3 a	85.0 a
5	5.0 a	90.0 a	9.0 ab	100.0 a	8.4 a	60.0 b	8.8 a	100.0 a
10	5.2 a	80.0 a	9.1 ab	90.0 a	7.5 a	79.0 ab	8.8 a	100.0 a
50	6.3 a	100.0 a	10.4 bc	100.0 a	7.9 a	73.5 b	8.2 a	94.0 a
200	7.3 a	95.0 a	12.4 c	84.5 a	9.3 a	18.8 c	14.0 b	75.0 a

[a] The experiment was begun with 20 first-instar larvae. Means within a column followed by the same letter are not significantly different ($P = 0.05$; Duncan's multiple-range test).

TABLE 4. EFFECT OF DIMBOA ON LIFE CYCLE OF *Eriopis connexa* IN ARTIFICIAL DIETS[a]

Treatment	Larvae		Pupae			Adult	
(μg DIMBOA/ g diet)	Duration (days)	Survival (%)	Duration (days)	Survival (%)	Weight (mg)	Time to reach adulthood (days)	Emergence (%)
0	29.2 a	70 a	4.4 a	100	7.0 a	33.6 a	100
2	32.4 a	55 a	4.8 a	100	6.1 a	37.3 a	100
5	31.0 a	55 a	4.5 a	100	6.5 a	35.5 a	100
10	30.6 a	55 a	4.3 a	100	6.1 a	34.8 a	100
50	32.8 a	60 a	5.3 a	100	6.7 a	38.0 a	100
200	43.0 b	10 b	4.5 a	100	6.1 a	47.5 b	100

[a] The experiment was begun with 20 first-instar larvae. Means within a column followed by the same letter are not significantly different ($P = 0.05$; Duncan's multiple-range test).

concentration of DIMBOA tested, the effect was statistically significant only for the highest concentration of DIMBOA. This concentration also decreased larval survival but had no effect on pupal survival nor on adult emergence.

Effect of Aphids Reared on DIMBOA-Containing Wheat Lines on E. connexa *Larvae.* The development time of *E. connexa* larvae differed significantly depending on the wheat cultivar on which their aphid prey had fed, the duration being longer in the case of the cultivar with an intermediate level of DIMBOA. Pupal developmental time was not affected by the level of DIMBOA in the wheat cultivar. Larval survival was lower with aphids that had fed on the wheat cultivar with the intermediate DIMBOA level (Table 5); aphid consumption was also lower in this cultivar (Table 6).

DISCUSSION

DIMBOA has been shown to be a feeding deterrent towards aphids. Thus, survival of aphids feeding on diets (Argandoña et al., 1983; Niemeyer et al., 1989b) or on wheat plants (Niemeyer et al., 1989b) differing in DIMBOA level showed a biphasic behavior: in the lower DIMBOA range survival was inversely correlated with DIMBOA concentrations while at the higher end survival was positively correlated with DIMBOA concentrations. Dual choice tests showed that aphids preferentially settled on leaves of wheat seedlings containing lower DIMBOA levels (Givovich and Niemeyer, 1991). Finally, electronic monitoring of aphid feeding behavior showed that fewer aphids reached the phloem, and those that did took longer to reach it in seedlings with higher DIMBOA levels

TABLE 5. DEVELOPMENT TIMES OF LARVAE AND PUPAE OF *E. connexa* REARED WITH APHIDS (*R. padi*) FED ON OATS AND WHEAT LINES CONTAINING DIFFERENT DIMBOA LEVELS[a]

		Development time (days)								
		Larvae						Larva to adult	Survival	
Plant	DIMBOA (μg/g fr. wt.)	I	II	III	IV	Total	Pupae	Total	Larvae	Pupae
Oat		2.1a	1.8a	2.1a	4.4a	10.4a	3.9a	14.3b	100	100
Millaleu	140	2.0a	2.0a	2.8b	3.6b	10.4a	4.0a	14.4b	98	100
Nobo	270	2.3b	1.8a	2.3a	4.3ab	10.7b	4.0a	14.7a	93	100
Maiten	440	2.5b	1.9a	2.3a	2.4c	9.1c	3.8a	13.9c	100	100

[a] The experiment was begun with 10 first-instar larvae. Means within a column followed by the same letter are not significantly different ($P = 0.05$; Duncan's multiple-range test).

TABLE 6. APHID CONSUMPTION BY *E. connexa* LARVAE OF APHIDS REARED ON OATS AND ON WHEAT LINES CONTAINING DIFFERENT LEVELS OF DIMBOA[a]

		Instar				
Plant	DIMBOA (μg/g fr. wt.)	1	2	3	4	Total
Oats		14.3ab	39.0a	27.6a	34.3a	115.2a
Millaleu	140	14.5a	38.8a	26.0b	33.7a	113.0b
Nobo	270	14.4ab	37.8b	26.3b	31.6c	110.1c
Maiten	440	14.0b	38.2b	26.2b	32.7c	111.5d

[a] The experiment was begun with 10 first-instar larvae. Means within a column followed by the same letter are not significantly different ($P = 0.05$; Duncan's multiple-range test).

than in those with lower ones (Givovich and Niemeyer, 1991). Hence, it appears that below a given DIMBOA level, the aphid ingests the compound, while above this level DIMBOA deters the aphid from feeding, leading to higher short-term survival rates.

An aphid feeding for 24 hr on a wheat seedling will accumulate DIMBOA in concentrations on the order of 1 μg/g aphid (Niemeyer et al., 1989b). Longer feeding times, as may occur under field conditions, should not radically affect this estimation since: (1) DIMBOA levels in the plant decrease as the plant develops (Argandoña et al., 1981), thus exposing the aphid to lower DIMBOA levels when feeding; (2) the instability of DIMBOA in aqueous solutions (Niemeyer et al., 1982) will hinder its accumulation; and (3) metabolization of

DIMBOA by the insect may occur, as has been shown in the case of a lepidopteran (Campos et al., 1989), which would also hinder its accumulation.

The lowest concentration of DIMBOA in diets tested on *E. connexa* is comparable with that expected in aphid bodies (Niemeyer et al., 1989b). This concentration led to a detectable, albeit not significant, increase of larval and pupal time periods of *E. connexa* with respect to control diet (Tables 3 and 4). When the predator fed on aphids, development times were also altered, being longest when the aphid prey had fed on the cultivar that had an intermediate DIMBOA level. An explanation of this finding is that these aphids were more deleterious to the predator. This is supported by the facts that: (1) two other cereal aphid species, *M. dirhodum* and *S. avenae*, feeding on wheat seedlings with intermediate DIMBOA levels accumulated the most DIMBOA in their bodies (Niemeyer et al., 1989b), and (2) *R. padi* feeding on wheat seedlings with intermediate DIMBOA levels accumulated the most DIMBOA (in glucosylated form) in their honeydew (Givovich et al., 1992). Alternatively, longer development times may have resulted from larvae ingesting fewer aphids (Table 6), which would still suggest that the compound in the plant was acting on the third trophic level, in this case through feeding deterrency. The fact that the development time of the predator significantly decreased when it fed on aphids from wheat seedlings containing high DIMBOA levels with respect to those containing low DIMBOA levels suggests that an increase in DIMBOA concentration in the plant, useful for aphid resistance, could result in the additional benefit of minimizing the effect of the toxin on the predator. This is a subtle and hitherto unreported mechanism in a tritrophic interaction between plant, herbivore, and predator (see Emden and Wratten, 1991).

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