

SECONDARY PLANT CHEMICALS IN APHID-HOST INTERACTIONS

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Introduction

Aphids damage plants by draining nutrients from them, by transmitting viral diseases, by inoculating toxins through their saliva, and by interfering with photosynthetic efficiency and providing a rich medium for fungal growth through their excretion products (Schepers 1989).

Control measures for aphids include, in the case of heteroecious species, measures at the primary host such as early defoliation, oil spray, pruning, and preservation of a habitat for predators. Migration to the secondary host may be prevented by the control of weeds that may act as a bridge, the application of behavior-modifying chemicals, and various ways of host plant masking. At the secondary host, control may be exerted by variations in the quality of the host, which may be achieved by manipulation of its nutrient value or its content in allelochemicals, commonly secondary plant metabolites (Harrewijn and Minks 1989), among other methods (van Emden and Wratten, this volume).

This paper deals with the role that secondary metabolites from plants play in aphid-plant relationships. Emphasis will be placed on the involvement of hydroxamic acids from cereals in aphid resistance.

Host Finding by Aphids: Sensing Plant Secondary Metabolites

The finding of the host by an aphid consists of a series of events, as summarized in Figure 1. Arrival at an area with potential host plants is a chance event depending to a large extent on aphids being carried by wind. Once in the neighbourhood of potential host plants, visual and olfactory

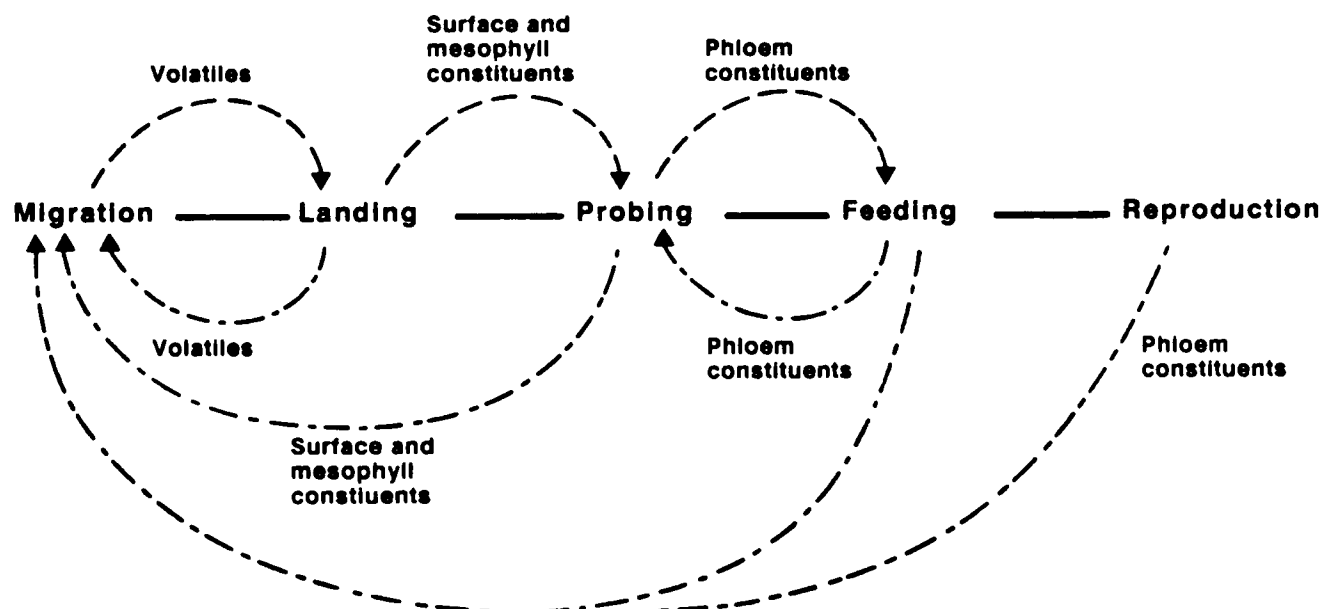


Fig. 1. Host finding by aphids: intervention of plant secondary compounds. - - - = attractive compounds or feeding stimulants; — — — = repellent, antifeedant or antibiotic compounds.

orientations play a more important role. Visual organs are present in all instars, and secondary compound eyes, which are more developed in adults, contain ommatidia which tend to be larger and more numerous in alatae, consistent with their migratory and host searching activities (Anderson and Bromley 1987). The number of ommatidia is limited and hence visual stimuli play a role only at close range (Harrewijn and Minks 1990). Olfactory organs are present on the antennae. Their number is also limited and thus olfaction also plays a role only at close range (Anderson and Bromley 1987).

After aphid alightment on a plant, surface chemicals become important in host acceptance. These may be components of the epicuticular lipid layer of the plant (Dillwith and Berberet 1990) or components in the trichomes of certain plant species (Gibson and Pickett 1983; Avé et al. 1987). The nature of these chemicals is perceived by chemoreceptors on the antennae (Bromley et al. 1979) and on the apex of the tibiae and the tarsi (Anderson and Bromley 1987).

The next stage in assessing the quality of a plant is the probing and tasting of inner plant components, which are carried out mainly by gustatory papillae in the epipharyngeal organ (Wensler and Filshie 1969; McLean and Kinsey 1985). Once the aphid reaches its final feeding site, normally the phloem (Pollard 1973), and provided it does not encounter toxic compounds in it (Molyneux et al. 1990) it will reproduce, its performance depending on the nutritional value of the sap, as reflected in its amino acid content (Wiktelius et al. 1990) and composition (Weibull 1988).

The relative importance of visual, olfactory and gustatory stimuli in host finding is related to the feeding habit of the aphid, and the particular morph under consideration. Thus, in polyphagous morphs, such as gynoparae of *Myzus persicae* (Sulzer) and *Aphis fabae* (Scopoli), and alate virginoparae of *Rhopalosiphum padi* (L.), visual stimuli play an important role (Hodgson and Elbakhiet, 1985). In oligophagous morphs, such as alatae of *Aphis gossypii* (Glover) (Pospisil, 1972) and *Cavariella aegopodii* (Scopoli) (Chapman et al., 1981), apterous virginoparae of *Cryptomyzus korschelti* (Börner) (Visser and Taanman, 1987) and alate virginoparae of *A. fabae*, and in monophagous morphs, such as gynoparae and males of *R. padi* (Pettersson 1970; Leather 1986), olfactory stimuli seem to prevail.

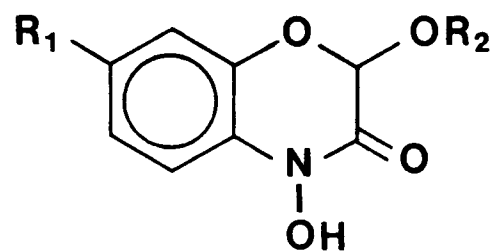
Plant secondary metabolites listed in Table 1 have been reported to be involved in aphid-plant interactions. The table includes volatiles or compounds giving rise to volatiles attracting aphids at close range, such as cyanogenic glucosides, and volatiles repelling them, such as E- β -farnesene; components of the plant wax layer which exert positive stimuli towards aphids, such as alkanes, or those which provoke negative stimuli, such as diketones; components in trichomes deleterious to aphids, such as 2-tridecanone; compounds in the mesophyll which stimulate colonization by aphids, such as certain phenolics, and those which deter them, such as hydroxamic acids; and finally phloem constituents which, depending on the specific aphid-plant combination, may act as positive or negative stimuli towards colonization by aphids, such as quinolizidine alkaloids.

These compounds, when they constitute a repellent stimulus or a source of toxicity, may in principle be manipulated by plant breeders to generate plants with enhanced barriers to aphid colonization. For this to be possible, not only the involvement of a given secondary metabolite must be determined, but an understanding of the interaction at the molecular level must be developed, and suitable parental germplasm for breeding must be encountered. If a modern bio-engineering approach is to be undertaken, knowledge of the genes involved in the accumulation (biosynthesis vs. degradation) of the compound and the associated gene physiology, must be secured.

One of the best described examples of plant secondary compounds involved in plant-aphid interactions are hydroxamic acids (Hx) (Fig. 2). They are a family of compounds of the 4-hydroxy-1,4-benzoxazin-3-one type present in the Gramineae, which show good promise as a defense mechanism in cereals (Niemeyer 1988).

Table 1. Principal classes of plant secondary compounds involved in aphid-host interactions

COMPOUNDS	PLANT	APHID	REFERENCE
Cyanogenic glucosides	<i>Prunus</i>	<i>R. padi</i> 1986	Petterson, 1973; Leather, 1986
Glucosinolates	<i>Brassica</i>	<i>Brevicoryne brassicae</i> (L.) <i>M. persicae</i> <i>Lipaphis erysimi</i> (Kaltenbach)	Petterson, 1973; Wensler, 1962 Weber <i>et al.</i> , 1986 Gill and Bakhetia, 1985
"Host plant odours"	<i>Stachis</i> <i>Cucurbita</i> , <i>Thunbergia</i>	<i>C. korschelti</i> <i>A. gossypii</i>	Visser and Taanman, 1987 Pospisil, 1972
Alkanes	<i>Vicia</i>	<i>Acyrtosiphon pisum</i> (Harris)	Klingauf, 1978
Diketones	<i>Triticum</i>	<i>S. avenae</i>	Lowe <i>et al.</i> , 1985
Phenols	<i>Vicia</i> , <i>Beta</i>	<i>A. fabae</i>	Jordens-Rittger, 1979
Phlorizin	<i>Malus</i>	<i>Aphis pomi</i> (DeGeer)	Montgomery and Arn, 1974
Alkaloids	<i>Nicotiana</i>	<i>R. maidis</i>	Abernathy and Thurston, 1969
2-Tridecanone	<i>Lycopersicon</i>	<i>A. gossypii</i>	Williams <i>et al.</i> , 1980
E- β -Farnesene	<i>Solanum</i>	<i>M. persicae</i>	Lapointe & Tingey, 1986; Avé <i>et al.</i> , 1987
Quinolizidine alkaloids	<i>Sarathamnus</i> <i>Lupinus</i> <i>Petteria</i> <i>Cytisus</i> <i>Lupinus</i>	<i>Acyrtosiphon spartii</i> (Koch) <i>A. pisum</i> <i>Aphis cytisorum</i> (Hartig) <i>Macrosiphon albifrons</i> \approx (Harris)	Smith, 1966 Wegorek and Krzymanska, 1971 Wink and Witte, 1985 Wink and Romer, 1986
Indol alkaloids	<i>Hordeum</i>	<i>S. graminum</i> , <i>R. padi</i>	Zúñiga and Corcuera, 1988
Phenolics	<i>Malus</i> <i>Rosa</i> <i>Populus</i>	<i>Eriosoma lanigerum</i> (Hausmann) <i>Macrosiphum rosae</i> (L.) <i>Pemphigus betae</i> (Doane)	Sen Gupta and Miles, 1975 (Hausmann) Miles, 1985 Zucker, 1982
Coumarins	<i>Vicia</i>	<i>Aphis craccivora</i> (Koch)	Mansour <i>et al.</i> , 1982
Cardiac glycosides	<i>Asclepiadaceae</i>	<i>Aphis nerii</i> (Boyer)	Rothschild <i>et al.</i> , 1970
Hydroxamic acids	<i>Gramineae</i>	<i>M. dirhodum</i> , <i>S. graminum</i> <i>S. avenae</i> , <i>R. padi</i> , <i>R. maidis</i>	Niemeyer, 1988; Leszczynski <i>et al.</i> , 1989



$R_1 = \text{H, CH}_3\text{O}$
 $R_2 = \text{H, glucosyl}$
 DIMBOA: $R_1 = \text{CH}_3\text{O, } R_2 = \text{H}$
 DIBOA: $R_1 = \text{H, } R_2 = \text{H}$

Fig. 2. Main hydroxamic acids in the Gramineae.

Hydroxamic Acids in Cereal Resistance to Aphids

Hydroxamic acids (Hx) were discovered over three decades ago in relation to fungal diseases of rye (Virtanen and Hietala, 1960). Later found in maize, they were associated with resistance to the European corn borer, *Ostrinia nubilalis* (Hübner). Breeding programs led to the production of maize cultivars with high Hx levels which were resistant to leaf feeding by the first brood of the borer (Grombacher et al. 1986; Guthrie et al. 1986).

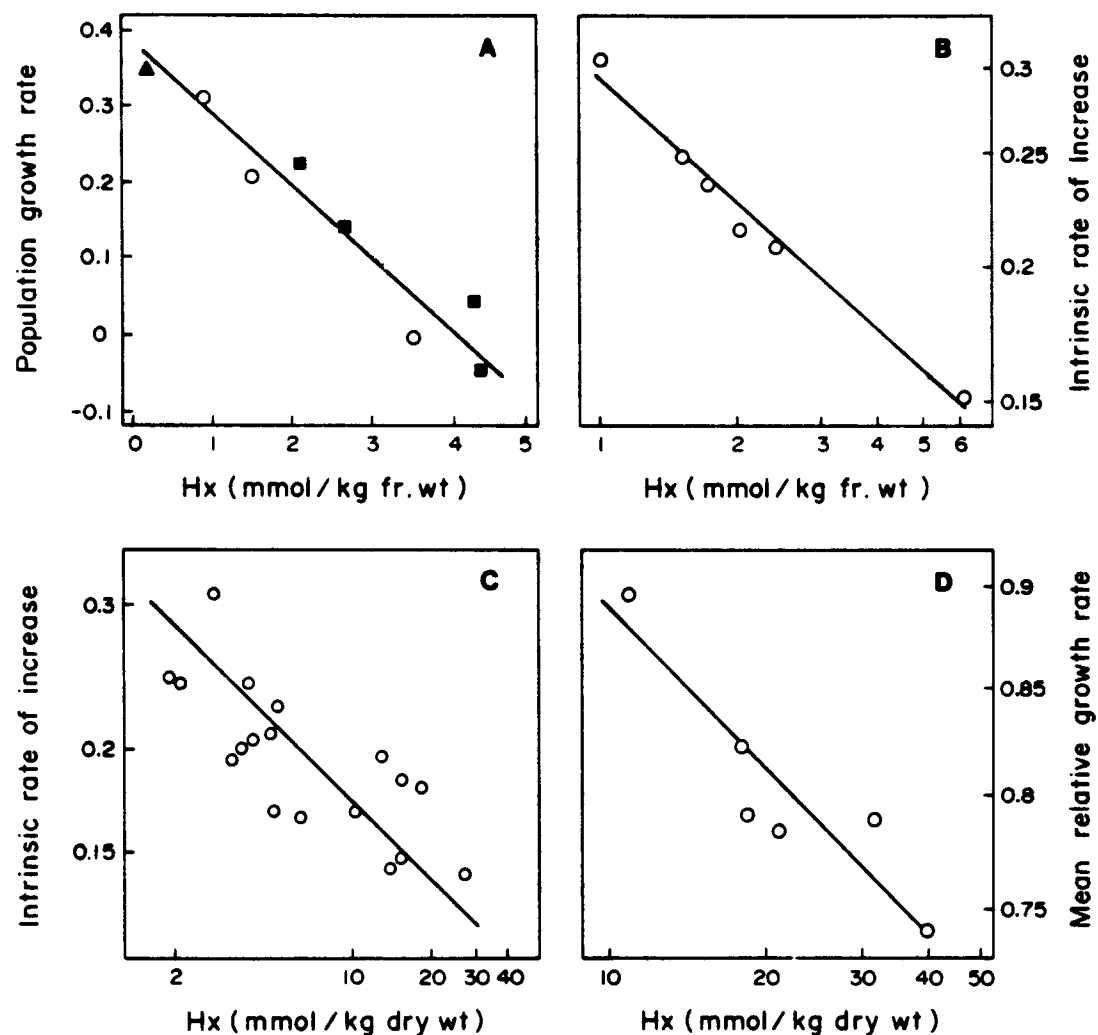


Fig. 3. Hydroxamic acid in plants and aphid population increase measured as population growth rate [A, ▲ = barley, ○ = wheat, ■ = rye] (Argandoña et al., 1980), intrinsic rate of natural increase [B and C] (Bohidar et al., 1986; Thackray et al., 1990a), or mean relative growth rate [D] (Thackray et al., 1990b).

The first work relating Hx with aphid performance refers to *Rhopalosiphum maidis* (Fitch) growing on different maize inbreds (Long et al. 1977). Inverse correlations occur between populations of aphids accumulated on plants and Hx levels in the plants, both in greenhouse and field experiments (Beck et al. 1983). Further studies on aphid performance on cultivated and wild Gramineae in relation to Hx levels during the past dozen years have further substantiated the correlations described. Figure 3 summarizes the data for *Metopolophium dirhodum* (Walker), *Sitobion avenae* (F.), *Schizaphis graminum* (Rondani) and *R. padi*, in which aphid performance is determined in three different ways: population growth rate (Argandoña et al. 1980; Corcuera et al. 1982), intrinsic rate of natural increase (Bohidar et al. 1986; Thackray et al., 1990a) and mean relative growth rate (Thackray et al. 1990b). Two of these correlations individually include widely different taxa, e.g. Figure 3A includes barley, rye and wheat, and Figure 3B includes tetraploid and hexaploid wheats: *Triticum durum*, *T. polonicum*, *T. dicoccum* and *T. aestivum*.

Incorporation of DIMBOA into excised barley leaves originally lacking Hx, and measurement of the performance of *M. dirhodum* on them, leads to a similar linear correlation (Argandoña et al. 1980). Moreover, survival of *R. maidis*, *S. graminum* and *M. dirhodum* decreases with increasing DIMBOA concentrations in artificial diets where aphids feed from (Corcuera et al. 1982), lending credibility to the interpretation that Hx are the causative factor in the correlations of Figure 3, and pointing to an antibiotic effect of Hx on aphids.

When *S. graminum* is allowed to feed for a short period of time from artificial diets containing different DIMBOA concentrations, and is then transferred to control diet without DIMBOA, mortality first increases and then decreases with increasing DIMBOA concentrations in the original diet (Argandoña et al. 1983). Additionally, the concentrations of DIMBOA found in *S. avenae* which had been feeding on artificial diets or wheat plants with increasing DIMBOA levels go through a similar maximum (Niemeyer et al. 1989).

Electronic monitoring of the feeding behavior of *S. graminum* in artificial diets containing different DIMBOA levels shows that the average ingestion period is inversely correlated with DIMBOA levels (Argandoña et al. 1983).

In dual choice tests between wheat cultivars differing in DIMBOA levels, *R. padi* shows a significant tendency to preferentially settle on those plants with lower DIMBOA levels. Electrical penetration graphs (Tjallingii 1990) showed that in wheat seedlings with higher DIMBOA levels fewer aphids reached the phloem within a given time, and they needed longer times to contact a phloem vessel than in those with lower levels (Figure 4) (Givovich and Niemeyer 1990). These experiments demonstrate a feeding deterrent effect of DIMBOA on aphids before the aphid reaches the phloem. Moreover, the time an aphid remains feeding in the phloem is independent of the DIMBOA level

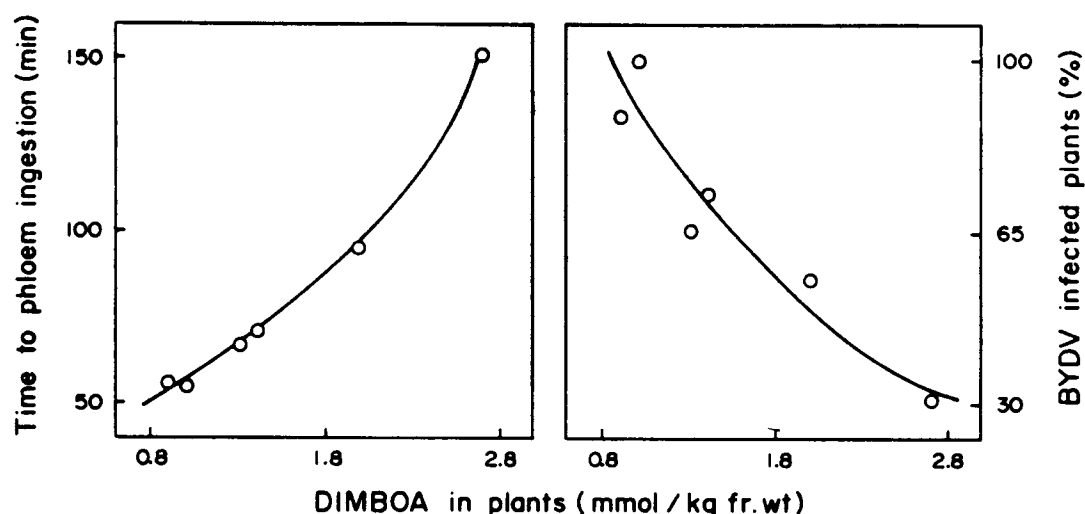


Fig. 4. Ability of *Rhopalosiphum padi* to reach the phloem and to infect with BYDV, plants of wheat cultivars with different levels of hydroxamic acids.

determined in the seedling. The antibiotic effect of DIMBOA described for aphids feeding on wheat plants, may be due to the effect of DIMBOA ingested prior to reaching the phloem or to levels in the phloem which result in antibiosis but are insufficient to provoke feeding deterency.

Feeding deterency by DIMBOA opens the possibility of these compounds bearing on transmission of barley yellow dwarf virus (BYDV) by aphids. When nymphs of *R. padi* carrying BYDV feed on seedlings of wheat cultivars with different DIMBOA levels, fewer seedlings are infected with BYDV in the high DIMBOA cultivars than in the low ones (Figure 4). In agreement with this finding, in a survey of 17 wheat lines in current use in Chile, BYDV tolerance was found in the six highest DIMBOA lines and BYDV susceptibility was found in the next nine lower DIMBOA lines. The two lines with the lowest DIMBOA levels were classified as tolerant, possibly reflecting some virus-host interaction preventing virus from establishing or replicating effectively (Givovich and Niemeyer 1990).

The search for conditions for the safe manipulation of Hx and for a molecular interpretation of its biological activities has led to detailed studies of their chemistry. The basis for the reactivity of DIMBOA is provided by the fast equilibration in solution of the hemiacetal (predominant) with an aldol. These molecules show organic functions which are highly reactive towards nucleophiles (Figure 5). Thus, thiols reduce the nitrogen atom producing a lactam and form hemithioacetals by addition to the aldehyde group (Atkinson et al. 1990), and amines form Schiff bases with both the aldehydic and the hydroxamic carbonyl groups (Pérez and Niemeyer 1989b). Furthermore, papain, a proteolytic enzyme with a highly reactive cysteine at the active site, is inactivated by DIMBOA by reaction of the hydroxamic nitrogen atom with the reactive sulphhydryl group (Pérez & Niemeyer 1989a), and α -chymotrypsin, a proteolytic enzyme with a hyper reactive serine at the active site, is inactivated by DIMBOA by reaction of the hydroxyl group of this serine, and possibly the amino group of lysine residues, with the hemiacetal (or aldol) (Cuevas et al. 1990).

These studies with model organic compounds and enzymes constitute the basis for the interpretation of the effect of DIMBOA on aphid enzymes. Acetylcholinesterases in insects are key enzymes in the transmission of nerve impulses and are the targets of organophosphorous and carbamate insecticides (Hoover 1980). Acetylcholinesterase has an essential serine at the active site. In addition, aphid cholinesterases have a catalytically important cysteine residue elsewhere (Zahavi et al. 1972; Manulis et al. 1981; Brestkin et al. 1985).

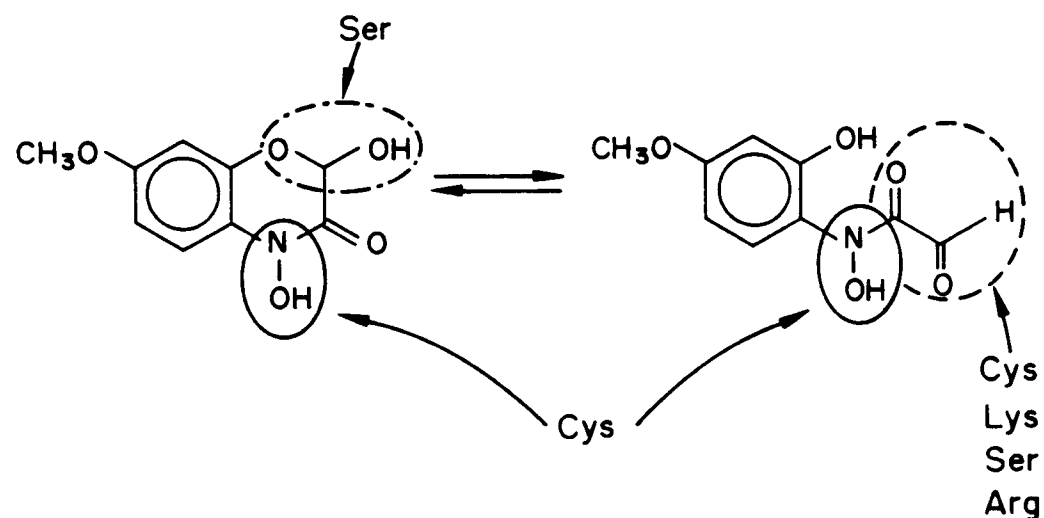


Fig. 5. Organic functions responsible for the reactivity of hydroxamic acids in solution. Abbreviations refer to aminoacid residues from enzymes.

Acetylcholinesterases isolated from *R. padi* show a pH optimum of 7 and are inhibited by thiol reagents, similar to results with acetylcholinesterases of other aphids. They are inactivated by DIMBOA, presumably by reaction of cysteine and serine residues with the nitrogen atom and the hemiacetal function. This inactivation may account for the antibiotic effects of DIMBOA on aphids (Cuevas and Niemeyer 1990).

Surveys of Hx levels in different taxa of the Gramineae (Zúñiga et al. 1983; Niemeyer 1988b; Thackray et al. 1990a) reveal variations of Hx levels in cultivated wheats ranging from 1 to 10 mmol/kg fr. wt at the age of highest accumulation in the seedling (Argandoña et al. 1981), and availability of wild grasses with unusually high levels of Hx, e.g. nearly 40 mmol DIMBOA/kg fr. wt in wild *Secale* species and 12 and 16 mmol DIBOA/kg fr. wt in wild *Critesion* and *Elymus* species, respectively (Copaja et al. 1990).

Additionally, DIBOA appears in all wild species examined in the genus *Hordeum*, but is absent from barley cultivars studied (Barría et al. 1990). The results provide a rationalization of earlier results on performance of *R. padi* in wild and cultivated barley (Weibull 1987).

It seems desirable to increase the content of Hx in agronomically interesting wheats. Genetic engineering appears as a valid alternative, provided that further knowledge is gained on the enzymology and molecular biology of these metabolites (Bailey and Larson 1989).

Given the very sophisticated way in which cereal aphids feed (Pollard 1973; Tjallingii 1990), it is essential to examine the tissue and sub-cellular localization of hydroxamic acids.

Hydroxamic acids are present in the intact plants as glucosides which are broken down to the active aglucones by endo β -glucosidases when the tissue is injured (Hofman and Hofmanová 1969). Since aglucones are also phytotoxic (Queirolo et al. 1983), it is expected that the hydrolytic enzymes are present in a compartment different from that containing the glucosides. It is desirable to study tissue and sub-cellular localization of β -glucosidases and to determine in which form these metabolites are ingested by aphids.

Although biological control and host plant resistance are often compatible and even complementary (Starks et al. 1972; Pimentel and Wheeler 1973; Schuster et al. 1976; van Emden and Wratten, this volume), it has been demonstrated that variation in host insects, in particular through variations in their host plants, may have dramatic effects on their predators and parasitoids (Salt 1941; Vinson 1976; Powell and Zhi-Li 1983; Budenberg and Powell 1988). These effects may even render incompatible efforts to increase plant antibiosis with other pest control management practices (Bergman and Tingey 1979; Campbell and Duffey 1979; Kennedy 1974). It would be desirable to examine the performance of aphid predators and parasitoids when they interact with aphids settled on plants containing different Hx levels.

Conclusions

Knowledge about the interaction of aphids with plants, in particular those in which aphids constitute a pest of crop plants, has grown mostly in the descriptive, phenomenological aspects. Only lately has the intimate nature of the interactions begun to be explored. The days seem not so distant when a rational, predictable, bio-engineering approach to crop improvement will be possible by enhancement of natural plant defenses.

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