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The Triticeae as sources of hydroxamic acids, secondary metabolites in wheat conferring resistance against aphids

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Hydroxamic acids of the 2,4-dihydroxy-1,4-benzoxazin-3-one type (DIBOA; DIMBOA = 7-methoxy derivative) play an important role in the resistance of wheat to aphids, through antibiosis and feeding deterrency. Screening of species of the tribe Triticeae has identified useful sources of hydroxamic acids for breeding programs to increase aphid resistance in wheat. It is shown that hydroxamic acids may be used as taxonomic markers. On this basis, it is suggested that *Triticum speltoides* is a likely donor of the B genome to hexaploid wheat.

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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).

The first demonstration of an inverse relationship between aphid performance and Hx concentrations was with *Rhopalosiphum maidis* (Fitch) growing on different maize inbreds (LONG et al. 1977). Since then, negative correlations have been described between Hx levels and performance of cereal aphids both in cultivated and in wild Gramineae, determined on the basis of infestation levels of the plants (BECK et al. 1983), population growth rate (ARGANDOÑA et al. 1980; CORCUERA et al. 1982), intrinsic rate of natural increase (BOHIDAR et al. 1986; THACKRAY et al. 1990a) or mean relative growth rate (THACKRAY et al. 1990b).

Similar negative correlations were obtained with *Metopolophium dirhodum* (Walker) feeding on excised barley leaves (originally lacking Hx) in which different levels of DIMBOA had been incorporated (ARGANDOÑA et al. 1980). Survival of cereal aphids decreased with increasing DIBOA or DIMBOA concentrations in artificial diets on which aphids fed (CORCUERA et al. 1982; ARGANDOÑA et al. 1983).

Dual choice tests between wheat cultivars differing in DIMBOA levels showed that *Rhopalosiphum padi* (L.) preferentially settled on seedlings with lower DIMBOA levels (GIVOVICH and NIEMEYER 1991). Electronic monitoring of aphid feeding behavior (TJALLINGII 1990) showed that fewer aphids reached the phloem within a given time, and they required longer times to contact a phloem vessel in wheat seedlings with higher DIMBOA levels (GIVOVICH and NIEMEYER 1991). This feeding deterrent effect has been shown to decrease transmission of barley yellow dwarf virus to wheat seedlings (GIVOVICH and NIEMEYER 1991).

These arguments led to the proposal of increasing hydroxamic acid levels in wheat plants in order to obtain increased resistance to aphids (NIEMEYER 1988a; WRATTEN et al. 1991). In this paper, results are presented from a wide range of screening trials in Triticeae. Germplasm useful for breeding programs aimed at increasing Hx levels in wheat, was identified. The data presented also show the potential of hydroxamic acids as chemotaxonomic markers within the Triticeae, and suggest that *Triticum speltoides* is the donor of the B genome of hexaploid wheat.

Materials and methods

Plant material

Seeds were obtained from Instituto de Investigaciones Agropecuarias (INIA), Chile; Plant Breeding International, Cambridge, UK; United States Department of Agriculture (Small Grains Collection and ARS Crops Research Laboratory, Logan, Utah); and University of Missouri-Columbia.

Tables 1 through 4 list the Triticeae species that were analysed. Since Hx levels vary with the age of the plant (ARGANDOÑA et al. 1980; ZUÑIGA et al. 1983; THACKRAY et al. 1990a), analyses were carried out on the aerial parts of seedlings at the age of maximal Hx level. This corresponded to 4- to 7-day old seedlings, depending on the accession studied.

The classification and nomenclature of the Triticeae have been the subject of much debate (DEWEY 1984; BAUM et al. 1987; GUPTA and BAUM 1989; JAUHAR and CRANE 1989; KELLOGG 1989). In this paper, the names of cultivated *Triticum* species follow the system of BRIGGLE (1980), of wild *Triticum* species, that of KIMBER (1983), and of perennial Triticeae, that of DEWEY (1984).

Table 1. Hydroxamic acid levels in cereals, mean ± standard error

Cereal	n*	Mean concentration (mmol/kg fr. wt)	
		DIBOA	DIMBOA
Wheat	52	0.13 ± 0.19	4.0 ± 2.1
Rye	4	15.4 ± 13.9	ND
Triticale	11	2.1 ± 1.4	2.4 ± 1.5
Barley	6	ND	ND

*n = Number of cultivars analyzed
ND = Not detected

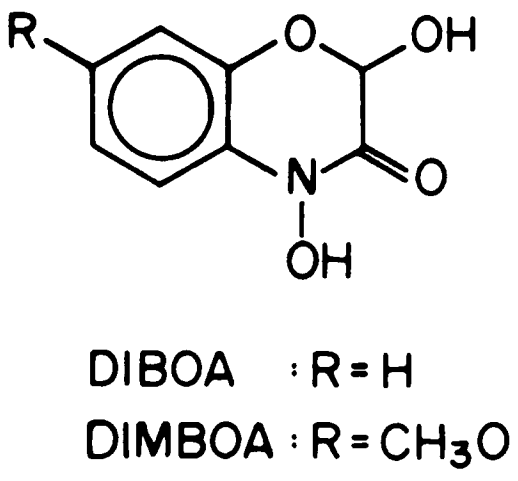

Table 2. Hydroxamic acid levels in cultivated *Triticum* species, mean ± standard error. Data mainly from NIEMEYER (1988a)

Species	Genome	n[a]	Mean Hx concentration (mmol/kg fr. wt)
T. monococcum[b]	A	4	0.6 ± 0.58
T. araraticum	AG	2	2.8 ± 0.71
T. timopheevi	AG	4	2.6 ± 0.74
T. carthlicum	AB	3	3.8 ± 0.43
T. dicoccum	AB	4	5.1 ± 0.96
T. polonicum	AB	4	5.4 ± 0.94
T. turgidum	AB	5	5.7 ± 2.46
T. zhukovskyi	AAG	2	1.8 ± 0.13
T. compactum	ABD	5	1.9 ± 0.55
T. macha	ABD	3	1.5 ± 0.91
T. spelta	ABD	5	2.5 ± 0.58
T. sphaerococcum	ABD	5	3.1 ± 0.44

[a] Number of accessions analyzed
[b] HPLC analysis of 2 accessions showed concentrations of DIBOA and DIMBOA of 0.14 and 0.08 mmol/kg fr. wt, respectively

Table 3. Hydroxamic acid levels in wild *Triticum* species, mean ± standard error

Species	Genome	n[a]	Mean concentration (mmol/kg fr. wt)	
			DIBOA	DIMBOA
T. tripsacoides	Mt	1	ND	ND
T. speltoides	S	3	ND	5.59 ± 1.55
T. bicorne	S[b]	4	0.25 ± 0.32	TR
T. sharonense	S	2	ND	0.17 ± 0.04
T. longissimum	S[l]	4	0.48 ± 0.44	TR
T. searsii	S[s]	2	1.27 ± 1.00	TR
T. dichasians	C	2	0.15 ± 0.15	ND
T. comosum	M	1	ND	1.09
T. uniaristatum	Un	2	3.78 ± 0.92	ND
T. umbellulatum	U	3	ND	TR
T. ovatum	U*M*	2	ND	0.40 ± 0.03
T. macrochaetum	U*M*	2	TR	TR
T. columnare	U*M*	2	ND	ND
T. triunciale	UC	2	TR	TR
T. kotschyi	U*S*	2	2.25 ± 1.11	0.30 ± 0.16
T. tauschii	D	3	0.18 ± 0.15	TR
T. cylindricum	DC	2	ND	ND
T. ventricosum	DUn	2	6.00 ± 0.42	ND
T. crassum	*DDM*	2	ND	ND
T. juvenale	*DMU*	2	ND	ND
T. syriacum	*DMS*	2	ND	ND

Limit of detection of the method: 0.1 mmol/kg fr. wt; TR = traces; ND = Not detected
[a] Number of accessions analyzed

Analysis of hydroxamic acids

Two different methods were used for Hx analysis. In the cultivated *Triticum* species of Table 2, a colorimetric method based on the formation of a complex between hydroxamic acids and $FeCl_3$ and

Table 4. Hydroxamic acid levels in perennial Triticeae, mean ± standard error. Data mainly from COPAJA et al. 1991a

Genus	n[a]	m[b]	Mean concentration (mmol/kg fr. wt)	
			DIBOA	DIMBOA
Agropyron	4	15	0.24 ± 0.18	0.22 ± 0.07
Critesion	7	19	2.27 ± 1.97	0.37 ± 0.18
Elymus	9	10	5.61 ± 4.51	0.40 ± 0.46
Elytrigia	1	2	0.11	0.26
Hordeum	5	5	1.25 ± 0.77	ND
Leymus	7	11	3.27 ± 3.02	1.08 ± 0.74
Secale	1[c]	3	31.14 ± 10.45	ND
Thinopyrum	6	13	0.68 ± 0.52	0.86 ± 0.53
Pascopyrum	1	3	0.14	1.13
Psathyrostachys	2	4	14.45 ± 5.98	ND
Pseudoroegneria	3	10	0.97 ± 0.26	0.12 ± 0.12

[a] Number of species analyzed
[b] Number of accessions analyzed
[c] Includes 3 subspecies of *S. montanum*
ND = Not detected.

its quantification by UV-Vis spectroscopy (BOHIDAR et al. 1986), was used (NIEMEYER 1988b). A method based on separation of hydroxamic acids by high performance liquid chromatography and quantification with a UV-Vis detector (NIEMEYER et al. 1989) was employed in the sets of species in Tables 1, 3 and 4 (COPAJA et al. 1991a,b).

Results and discussion

Hydroxamic acids as chemotaxonomic markers

The variations observed both in total and in relative concentrations of hydroxamic acids within different taxa in the Triticeae suggest they might be useful taxonomic markers. Support for this hypothesis was provided by data from cereals and from wild *Triticum* species.

While bread wheat (genome ABD) contains higher concentrations of DIMBOA than of DIBOA (COPAJA et al. 1991b), and rye (genome R) contains only DIBOA, the man-made hybrid triticale (genome AB(D)R) contains both DIBOA and DIMBOA (Table 1), thus reflecting its genome constitution. Similar effects appear in the comparison of DIBOA and DIMBOA concentrations in diploid and polyploid wild *Triticum* species. Thus, the C genome of *T. dichasians*, the D genome of *T. tauschii*, and the U genome of *T. umbellulatum* all lead to low or undetectable DIBOA levels; and the CD genomic combination of *T. cylindricum* and the UC genomic combination of *T. triunciale* also lead to undetectable DIBOA levels. On the other hand, the Un genome of *T. uniaristatum* may be associated with the accumulation of high levels of DIBOA in *T. ventricosum* (DUn genome).

Traditional taxonomic affinities among the perennial Gramineae are also reflected in hydroxamic acid levels (Table 4). The genera *Elymus* and *Leymus* constituted a single genus in the traditional treatment of the tribe (HITCHCOCK 1951) and both produce high levels of DIBOA. The genera *Pseudoroegneria*, *Elytrigia*, and *Thinopyrum*, traditionally considered within the broad genus *Agropyron* (DEWEY 1984; KELLOGG 1989; TZVELEV 1976), all show low levels of both hydroxamic acids.

Hexaploid wheat is an amphiploid containing genomes A, B, and D (KERBY and KUSPIRA 1987). While it is clear that *T. tauschii* is the donor of the D genome (GILL and KIMBER 1974; FERNANDEZ DE CALEYA et al. 1976; JONES et al. 1982), and that *T. monococcum* is the donor of the A genome (FERNANDEZ DE CALEYA et al. 1976; JONES et al. 1982), there has been much debate over the origin of the B genome. There is agreement that the putative donor belongs to the *Sitopsis* section of the genus (S genome). However, different techniques have led to variable conclusions regarding the likely candidate: *T. speltoides* (SARKAR and STEBBINS 1956; RILEY et al. 1958; REES and WALTERS 1965; JAASKA 1978; BAHRMAN et al. 1988), *T. bicorne* (SEARS 1956), *T. sharonense* (KUSHNIR and HALLORAN 1981), *T. longissimum* (VITTOZI and SILANO 1976; GERLACH et al. 1978; TSUNEWAKI and OGIHARA 1983) and *T. searsii* (FELDMAN 1978; NATH et al. 1983, 1984; THOMPSON and NATH 1986). Tetraploid wheats (genome AB) accumulate high levels of DIMBOA and low levels of DIBOA (COPAJA et al. 1991b). Since the A genome of *T. monococcum* is associated with the accumulation of low levels of both hydroxamic acids (Table 2), it seems unlikely that the donor of the B genome is *T. bicorne*, *T. longissimum*, or *T. searsii*, which produce mainly DIBOA, in relatively low quantities (Table 3). *T. sharonense* contains only low concentrations of DIMBOA and, hence, seems also an unlikely candidate. The data presented in Table 3 point to *T. speltoides* as the most likely putative donor of the B genome of wheat, since it contains high levels of DIMBOA. The nature and quantity of hydroxamic acids found in species of the Sitopsis section allow a separation into *T. speltoides* (high DIMBOA levels) on one hand, and *T. bicorne*, *T. sharonense*, *T. longissimum*, and *T. searsii*

(low DIBOA and DIMBOA levels) on the other. This finding agrees with earlier dendrograms based on similarities of two-dimensional gel electrophoresis of seedling proteins of species of the Sitopsis section (BAHRMAN et al. 1988). The lower levels of hydroxamic acids in hexaploid wheat relative to durum wheats might be attributed to the low levels found in *T. tauschii*, the donor of the D genome of hexaploid wheat.

Sources of hydroxamic acids for wheat breeding

Within the common wheats, durum wheats showed substantially higher concentrations of Hx than did bread wheats (Table 2). Given the similar toxicity of both hydroxamic acids for aphids (ZUÑIGA et al. 1983), the genome of rye seems a promising candidate for the transfer of aphid resistance to wheat.

Particularly interesting genomes as sources of hydroxamic acids are the S genome of *T. speltoides* (DIMBOA) and the Un genome of *T. uniaristatum* and the N genome of the genus *Psathyrostachys* (DIBOA). Crosses have been shown to be possible between wheat and all the perennial genera of the Triticeae, with the exception of *Psathyrostachys*. This has allowed the transfer of useful agronomical traits to wheat (SHARMA and GILL 1983; DVORAK et al. 1985; STOREY et al. 1985). This genus seems particularly promising as a source of DIBOA. Further work should be directed to the possibility of crossing this species with wheat.

Variation in whole plant concentration of Hx during phenological development may limit the usefulness of this factor as a source of aphid resistance; after a steep increase soon after germination, it decreases considerably (ARGANDOÑA et al. 1981; THACKRAY et al. 1990a). However, it has been shown, repeatedly, that the youngest tissue in a wheat plant retains a high concentration of Hx (ARGANDOÑA et al. 1980; ARGANDOÑA et al. 1981; ZUÑIGA et al. 1983; NIEMEYER 1988b; THACKRAY et al. 1990a; COPAJA et al. 1991a). The concentration of Hx in areas of sensitive new growth may have important consequences for defense against aphids such as *Sitobion avenae*, which feeds on flag leaves and ears (WRATTEN 1975) and *R. padi*, which is a seedling pest in western Europe (VICKERMAN and WRATTEN 1979). A negative correlation has been found between mean relative growth rate of *S. avenae* and Hx concentration in flag leaves of wheat plants (LESZCZYNSKI et al. 1989).

Emergence of resistant biotypes of aphids is a common feature of aphid-host plant interactions. Hence, a breeding program of wheat aimed at aphid resistance should be based on a broad range of factors which confer stability to overall resistance. Non-glaucousness has been described as an antixenotic factor in wheat against *S. avenae* (LOWE et al. 1985). Phenols have been shown to play a role in wheat resistance against *S. avenae* (LESZCZYNSKI et al. 1989). Incorporation of these characteristics, together with high levels of hydroxamic acids, should be among the aims of wheat breeding programs (WRATTEN et al. 1991).

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