

## Prospects for exploitation of disease resistance from *Hordeum chilense* in cultivated cereals

D. RUBIALES<sup>1</sup>, R. E. NIKS<sup>2</sup>, T. L. W. CARVER<sup>3</sup>, J. BALLESTEROS<sup>1</sup> and A. MARTÍN<sup>1</sup>

<sup>1</sup> Instituto de Agricultura Sostenible, C.S.I.C., Córdoba, Spain

<sup>2</sup> Department of Plant Breeding, AJ Wageningen, The Netherlands

<sup>3</sup> Institute of Grassland and Environmental Research, Aberystwyth, UK

Rubiales, D., Niks, R. E., Carver, T. L. W., Ballesteros, J. and Martín, A. 2001. Prospects for exploitation of disease resistance from *Hordeum chilense* in cultivated cereals. — *Hereditas* 135: 161–169. Lund, Sweden. ISSN 0018-0661.

*Hordeum chilense* is a South American wild barley with high potential for cereal breeding given its high crossability with other members of the Triticeae. In the present paper we consider the resistance of *H. chilense* to several fungal diseases and the prospects for its transference to cultivated cereals.

All *H. chilense* accessions studied are resistant to the barley, wheat and rye brown rusts, the powdery mildews of wheat, barley, rye and oat, to Septoria leaf blotch, common bunt and to loose smuts, which suggests that *H. chilense* is a non-host of these diseases. There are also lines resistant to wheat and barley yellow rust, stem rust and to *Agropyron* leaf rust, as well as lines giving moderate levels of resistance to Septoria glume blotch, tan spot and Fusarium head blight. Some *H. chilense* lines display pre-appressorial avoidance to brown rust. Lines differ in the degree of haustorium formation by rust and mildew fungi they permit, and in the degree to which a hypersensitive response occurs after haustoria are formed.

Unfortunately, resistance of *H. chilense* to rust fungi is not expressed in tritordeum hybrids, nor in chromosome addition lines in wheat. In tritordeum, *H. chilense* contributes quantitative resistance to wheat powdery mildew, tan spot and loose smut. The resistance to mildew, expressed as a reduced disease severity, is not associated with macroscopically visible necrosis. Hexaploid tritordeums are immune to Septoria leaf blotch and to common bunt although resistance to both is slightly diluted in octoploid tritordeums. Studies with addition lines in wheat indicate that the resistance of *H. chilense* to powdery mildew, Septoria leaf blotch and common bunt is of broad genetic basis, conferred by genes present on various chromosomes.

D. Rubiales, Instituto de Agricultura Sostenible, C.S.I.C., Apdo. 4084, E-14080 Córdoba, Spain. E-mail: ge2ruozd@uco.es

*Hordeum chilense* Roem. et Schult is an extremely polymorphic, diploid wild barley that occurs exclusively in Chile and Argentina. After *H. vulgare/ spontaneum* and *H. bulbosum*, *H. chilense* is the species of the genus with the highest potential for cereal breeding purposes, given its high crossability with other members of the Triticeae tribe (*Triticum*, *Hordeum*, *Secale* and *Agropyron*) and its agronomically interesting characteristics (MARTÍN and CUBERO 1981; MARTÍN et al. 1996, 2000).

Plant geneticists have been interested in hybridising barley with wheat for more than 100 years but have had little success (KRUSE 1973). No fertile wheat × *H. vulgare* amphiploids have been produced even after many attempts (FEDAK 1992). In contrast, fertile amphiploids with wheat were easily produced using *H. chilense*. *H. chilense* has also been successfully hybridised with *Hordeum*, *Secale* and *Agropyron* species (MARTÍN and CUBERO 1981; MARTÍN et al. 1996, 1998, 2000). Addition, translocation and substitution lines of *H. chilense* in wheat, and addition lines in rye have been obtained. Clearly, these might be used as bridges to transfer useful traits to cultivated cereals, and potentially, disease resistance is one such valuable trait. In the present paper we will study and

discuss the level of resistance of a collection of *H. chilense* accessions to a range of diseases and its expression in hybrids, amphiploids and chromosome addition lines with cereals.

## RESULTS AND DISCUSSION

### Resistance to rusts

*H. chilense* is resistant to the barley and wheat brown rusts (*Puccinia hordei* and *P. triticina*, respectively) (RUBIALES et al. 1991, 1992b, 1993b; RUBIALES and NIKS 1992b) (Tables 1, 3). Certain *H. chilense* lines are also resistant to *P. agropyrina*, to wheat and barley yellow rusts (*P. striiformis* ff.spp. *tritici* and *hordei*, respectively) (RUBIALES et al. 1991; RUBIALES and NIKS 1992b) (Tables 2, 3) and to wheat stem rust (*P. graminis*) (Table 1). Several mechanisms limiting rust disease development operate in *H. chilense*.

Leaf surface characteristics can hamper the ability of urediniospore germ tubes to find and to penetrate stomata. This has only recently been reported to occur to a limited extent in certain *H. vulgare* mutants (RUBIALES et al. 2002) and such disease avoidance has not been documented in wheat. On some *H. chilense* lines, however, brown rust fungi form ap-

pressorium with very low frequency (RUBIALES and NIKS 1992a, 1996). This was attributed to heavy wax encrustation obscuring stomata so that germ tubes fail to recognise and respond to stomatal contact by differentiating appressoria (RUBIALES and NIKS 1996; VAZ PATTO and NIKS 2001). The trait seems to be inherited quantitatively. Three QTLs for avoidance have been identified and mapped to chromosomes 1, 3' and 5 (VAZ PATTO 2001). Morphology

and AFLP markers suggest that three *H. chilense* ecotypes can be recognised, one of which has a very high level of avoidance (VAZ PATTO et al. 2001). Avoidance has also been detected in other *Hordeum* accessions (*H. brachyantherum*, *H. marinum*, *H. parodi* and *H. secalinum*) and, recently, in *eceriferum* mutants of *H. vulgare*, but not in commercial cultivated barley or in accessions of other Triticeae genera (RUBIALES et al. 1996c, 2002).

Table 1. Field reaction of *H. chilense* accessions<sup>1</sup> to cereal pathogens

	Disease severity						
	Yellow rust <sup>2</sup>	Brown rust <sup>2</sup>	Stem rust <sup>3</sup>	Net blotch <sup>4</sup>	Powdery mildew <sup>2</sup>	Scald <sup>2</sup>	Septoria leaf blotch <sup>2</sup>
	<i>Puccinia striiformis</i>	<i>Puccinia triticina</i>	<i>Puccinia graminis</i>	<i>Pyrenophora teres</i>	<i>Blumeria graminis</i>	<i>Rhynchosporium secalis</i>	<i>Mycosphaerella graminicola</i>
H1	47	0	34	0	0	0	0
H7	19	0	14	0	0	0	0
H8	6	0	16	0	0	0	0
H10	27	0	15	0	0	0	0
H11	21	0	3	0	0	0	0
H12	50	0	25	0	0	0	0
H13	63	0	32	0	0	0	0
H14	10	0	40	0	0	0	0
H16	42	0	24	0	0	0	0
H17	22	0	12	0	0	0	0
H34	11	0	6	0	0	0	0
H35	50	0	20	0	0	0	0
H38	20	0	13	0	0	0	0
H39	21	0	21	0	0	0	0
H41	15	0	65	0	0	0	0
H46	32	0	24	0	0	0	0
H47	40	0	25	0	0	0	0
H50	6	0	32	0	0	0	0
H51	21	0	42	0	0	0	0
H52	30	0	29	nd	0	0	0
H54	33	0	26	0	0	0	0
H55	18	0	65	0	0	0	0
H56	35	0	25	nd	0	0	0
H57	30	0	46	0	0	0	0
H58	22	0	25	0	0	0	0
H59	45	0	13	0	0	0	0
H60	50	0	20	0	0	0	0
H61	30	0	20	nd	0	0	0
H64	58	0	50	nd	0	0	0
H68	26	0	40	nd	0	0	0
H74	17	0	32	nd	0	0	0
H75	26	0	11	0	0	0	0
H80	3	0	13	nd	0	0	0
H84	40	0	22	nd	0	0	0
H89	51	0	1	0	0	0	0
H93	63	0	30	nd	0	0	0
Susceptible control	70	50	20	20	30	40	40

<sup>1</sup> Origin of the accessions are described by VAZ PATTO et al. (2001).

<sup>2</sup> Average of DS obtained in 3 field seasons, at 2 locations, 2–3 replications location.

<sup>3</sup> Average of DS obtained in 2 field seasons at Córdoba, 3 replications per season.

<sup>4</sup> Average of 2 field seasons at Córdoba, 3 replications per season.

Table 2. Infection type<sup>1</sup> of *H. chilense* accessions to races of yellow rusts

	<i>P. striiformis</i> f.sp. <i>tritici</i>						<i>P. striiformis</i> f.sp. <i>hordei</i>				
	6E16	39E134	107E139	47E142	110E143	237E141	82-6	24	84-3	F24	Bolivia
H1	7	7	0,7	3	4	4	nd	8	8	7	6
H7	1	1	0	0	0	0	1	2	1	1	2
H8	1	6	nd	nd	nd	nd	nd	nd	nd	nd	nd
H11	8	8	nd	nd	nd	nd	nd	nd	nd	8	3
H12	7	4	6	4	5	nd	8	8	nd	6	6
H13	7	0	7	4	5	5	8	8	7	7	7
H16	6	nd	3,7	4	4	nd	4	7	7	nd	7
H17	2	0	0	0	0	0	1	1	1	1	1
H34	0	nd	nd	nd	nd	8	nd	nd	5	0	1
H35	6	nd	nd	nd	4	7	nd	nd	nd	nd	nd
H47	8	nd	nd	nd	nd	nd	nd	nd	nd	nd	nd
H55	nd	2	nd	nd	3	0d	4,7	nd	1	6	2
H61	2	3	nd	nd	nd	nd	nd	nd	nd	nd	nd
H74	8	nd	nd	nd	nd	nd	nd	nd	nd	0	2

<sup>1</sup> Infection type (IT) in seedling stage according to MCNEAL et al. (1971).

Table 3. Infection type<sup>1</sup> of *H. chilense* accessions to races of brown rusts

	<i>P. triticina</i>					<i>P. hordei</i>			<i>P. agropyrina</i>	<i>P. recondita</i> f.sp. <i>recondita</i>	
	85-31	82-1	85-20	Felix	Flamingo	60-3-1	79-2	83-3	1-2-1		
H1	1 <sup>1</sup>	0	0	0	1	1	nd	1	1	1-3	0-1
H7	1	0	1	0	0	1	1	1	1	1	0
H8	nd	nd	nd	nd	1-3	nd	nd	nd	1	7-8	0-1
H10	nd	nd	nd	nd	6	nd	nd	nd	1	6-7	0
H11	nd	nd	nd	nd	1-3	nd	nd	nd	0	0	0-1
H12	0	0	0	0	1	1	1	1	3	1	0-2
H13	0	0	0	0	1	1	nd	1	1-3	1	0-1
H16	nd	0	0	0	1-3	1	nd	1	0-1	6-7	0
H17	1	0	0	0	0-1	1	1	1	1	1-3	0
H34	1	nd	nd	0	0-1	1	1	1	nd1	5-6	0
H35	nd	nd	nd	nd	1	nd	nd	nd	1	7	0
H47	nd	nd	nd	nd	0-1	nd	nd	nd	0	nd	nd
H55	1	nd	nd	0	0-1	1	0	1	0	nd	0
H61	nd	nd	nd	nd	1	nd	nd	nd	0-1	nd	0
H74	nd	nd	nd	nd	0	1	nd	nd	0	0-2	0

<sup>1</sup> Infection type (IT) in seedling stage according to MCNEAL et al. (1971).

*H. chilense* accessions also differ in the level of prehaustorial resistance to brown rust fungi, as expressed by the level of early aborted colonies not associated with host cell necrosis (Table 4) (RUBIALES and NIKS 1992b). The response was to some extent rust non-specific, being particularly high in some accessions (H11, H17, H55) (Table 4) to all brown rusts studied. This suggests that these accessions have higher levels of general defence against rust fungi than the other accessions. The extent of the prehaustorial resistance depends on the rust species, being particularly high against the rye leaf rust fungus, *P. recondita* f.sp. *recondita*. This suggests that

the various rust fungi differ in their ability to negate general defence mechanisms.

The tritordeums are as resistant to the barley brown and yellow rust fungi as the their wheat parent (Table 6). Tritordeum lines may be susceptible to some and resistant to other races of wheat brown, yellow and stem rust, and of agropyron brown rust. This, however, depends on the wheat parental genotype and not on characters carried by the *H. chilense* genome (RUBIALES et al. 1991, 1992b; RUBIALES and NIKS 1992b). Furthermore, the resistance of *H. chilense* to rusts was not expressed in chromosome addition lines in wheat (D. Rubiales, unpubl.). The

effect of the resistance present in *H. chilense* to rust fungi is minimal in tritordeum: when a large collection of lines were screened over several years, brown rust severity tended to be lower in tritordeum than in wheat, but slightly higher for yellow rust. There are, however, indications that the tritordeums from particular *H. chilense* lines (H7 and H17, highly resistant to all races tested, Table 2) show slightly greater yellow rust resistance than the tritordeums from other *H. chilense* lines (H1 and H12). So, although the effects of *H. chilense* resistance are suppressed in tritordeum, there might still be a small, but useful, role of the *H. chilense* background in tritordeum (D. Rubiales, unpubl.). Suppression of rust resistance due to intergenomic interactions has previously been reported in cereals. Suppressors may possibly be eliminated through induction of mutations as has been reported for the 7DL suppressor locus of wheat 'Canthatch' (KERBER 1991) that inhibited resistance to stem rust.

Although the rust resistance of *H. chilense* is not strongly expressed in tritordeum, this is not true in crosses with rye (RUBIALES et al. 1993c). A hybrid and an amphiploid of *H. chilense* with rye expressed hypersensitivity to rye leaf rust (reduction in the infection type from 9 to 2).

#### Resistance to powdery mildew

*H. chilense* is resistant to the powdery mildew fungi of wheat, barley, rye and oat (*Blumeria graminis* ff.spp. *tritici*, *hordei*, *secalis* and *avenae*, respectively) (RUBIALES et al. 1993a; RUBIALES and CARVER 2000). All accessions were highly resistant to all

ff.spp. studied. A range of different mechanisms appeared to be responsible for mildew resistance. Relatively large differences between accessions were detected in penetration resistance and the frequency of cell death in response to attack. Resistance to penetration of living cells was extremely high in certain accessions (H11, H47, H49 and H51) (Table 5). In the majority of cases, successful penetration led to death of the infected cell and cessation of fungal development. The formation of haustoria occurs very infrequently in *H. chilense*, and when haustoria are formed, most epidermal cells containing the haustoria die soon (RUBIALES and CARVER 2000).

Tritordeum is resistant (infection type 0) to barley and rye powdery mildew (RUBIALES et al. 1993a,c) and *H. chilense* contributes quantitative resistance to tritordeum against wheat powdery mildew (RUBIALES et al. 1993a) (Table 6). Field trials showed that disease severity was consistently lower in tritordeum than in its wheat parent. Inoculating detached leaves with several isolates showed that there was a considerable reduction in numbers of wheat mildew colonies on tritordeum although the infection type was similar to that of the wheat parental line. The tetraploid tritordeum had a 20× reduction of infection frequency compared to its wheat parent; hexaploid tritordeums had a 7–14× reduction; and octoploid tritordeums a 1.5–2.5× reduction (RUBIALES et al. 1993a)

Quantitative resistance to wheat mildew was also expressed in various addition lines of *H. chilense* chromosomes in wheat. Different addition lines showed different degrees of reduction in wheat

Table 4. Levels of prehaustorial resistance<sup>1</sup> to leaf rusts in *H. chilense* accessions

	<i>P. hordei</i>	<i>P. agropyrina</i>	<i>P. triticina</i>	<i>P. recondita</i> f.sp. <i>recondita</i>	overall
H55	48	nd	64	92	68
H11	68	55	37	94	64
H17	62	59	55	80	64
H7	33	43	48	92	54
H10	46	27	15	100	47
H34	19	22	56	87	46
H74	43	52	33	47	44
H46	9	nd	77	nd	43
H47	20	nd	62	nd	41
H61	10	nd	30	75	38
H16	9	33	28	76	36
H8	29	5	22	84	35
H12	8	6	43	81	34
H1	10	10	28	74	30
H13	8	10	27	72	29
H35	13	25	26	46	27
Overall	27	29	41	79	

<sup>1</sup> Estimated as the percentage of early aborted colonies not associated with host cell necrosis.

Table 5. Levels of prehaustorial resistance<sup>1</sup> to powdery mildews in *H. chilense* accessions

	<i>B. graminis</i> f.sp. <i>hordei</i>	<i>B. graminis</i> f.sp. <i>tritici</i>	<i>B. graminis</i> f.sp. <i>avenae</i>	overall
H51	24	54	53	43
H11	30	45	47	41
H47	42	32	29	34
H49	15	34	46	32
H35	16	34	30	27
H7	13	31	34	26
H17	13	32	28	24
H8	17	22	23	21
H12	13	23	20	19
H1	16	22	15	18
H13	15	26	17	19
H34	10	21	16	16
H46	16	19	13	16
Overall	18	30	29	

<sup>1</sup> Estimated as the percentage of germlings with mature appressoria that failed to penetrate epidermal cells and not causing cell death.

mildew severity and this was not associated with a visible necrotic response. Resistance factors effective against wheat mildew isolates from two different locations in Europe were present on chromosomes 5H<sup>ch</sup>, 6H<sup>ch</sup> and 7H<sup>ch</sup>, but other factors, present on chromosomes 1H<sup>ch</sup>S, 2H<sup>ch</sup>α, and 4H<sup>ch</sup>, were effective against only one isolate (RUBIALES et al. 2001).

Thus, the evidence indicates that *H. chilense* may provide new sources of useful resistance to powdery mildew.

#### Resistance to *Septoria* diseases

Both *H. chilense* and tritordeum are resistant to *Mycosphaerella graminicola* (anamorph *Septoria tritici*) the causal agent of Septoria leaf blotch (RUBIALES et al. 1992a). Seedling tests under controlled conditions where plants were inoculated with isolates from both bread and durum wheat, and experiments with mature, field-grown plants indicated that all hexaploid tritordeums were immune to leaf blotch. Octoploid tritordeums allowed some disease development but considerably less than their respective bread wheat parental lines (RUBIALES et al. 1992a). Resistance in octaploid tritordeum was not associated with plant height but it was associated (to some extent) with lateness.

Tests on addition lines indicate that resistance is conferred by gene(s) on chromosome 4H<sup>ch</sup> and to a less extent by genes on chromosomes 5H<sup>ch</sup>, 6H<sup>ch</sup> and 7H<sup>ch</sup> (RUBIALES et al. 2000). This resistance might be particularly valuable when transferred to wheat, particularly to durum wheat, where little resistance to *M. graminicola* exists.

Some *H. chilense* and tritordeum lines are susceptible to *Phaeosphaeria nodorum* (anamorph *Stagono-*

*spora nodorum* [syn. *Septoria nodorum*]), the causal agent of Septoria glume blotch (RUBIALES et al. 1996a). Nevertheless, seedling and field experiments showed that various tritordeum lines were more resistant than their wheat parental lines. There was a slight reduction of the resistance at the higher ploidy level, but this was not as marked as for *M. graminicola*. Tritordeum resistance to *Ph. nodorum* was associated with lateness but not with tall plant stature. It should therefore be possible to breed short octoploid tritordeum lines with resistance to both Septoria diseases, and it should prove relatively straightforward to produce hexaploid tritordeums with resistance to both.

#### Resistance to bunts and smuts

*H. chilense* is highly resistant to common bunt (*Tilletia caries*) (RUBIALES et al. 1996b). This resistance is completely expressed in hexaploid tritordeum lines, although slightly diluted in octoploid lines (average of 3 × reduction in % of infected spikes) and in addition lines in bread wheat. Resistance is conferred by gene(s) on chromosome 7H<sup>ch</sup> and to less extent by genes on chromosome 6H<sup>ch</sup> (RUBIALES and MARTÍN 1999). It is likely that the resistance would be more strongly expressed if the chromosome(s) were added to durum wheat because of its tetraploid nature. Thus, the *H. chilense* resistance could be very helpful in breeding durum wheat which is becoming an increasingly important crop in the Mediterranean and other world regions.

Resistance to Karnal bunt (*T. indica*) was described by CHAUHAN and SINGH (1997) in two *H. chilense* accessions. Three secondary tritordeum lines with the same pedigree were studied. One of these

Table 6. Reaction of *H. chilense*, wheat and tritordeum to several pathogens

Pathogen or pest	Reaction of		References
	<i>H. chilense</i>	Wheat <sup>a</sup>	
<i>Puccinia striiformis</i> f.sp. <i>tritici</i>	R to S	R to S	Rubiales et al. 1991, 1993b
<i>Puccinia striiformis</i> f.sp. <i>hordei</i>	R to S	R	Rubiales et al. 1991, 1993b
<i>Puccinia triticina</i>	R	R to S	Rubiales et al. 1991, 1993b
<i>Puccinia recondita</i> f.sp. <i>recondita</i>	R to S	R	Rubiales et al. 1993b
<i>Puccinia agropyrina</i>	R	R	Rubiales et al. 1991, 1993b
<i>Puccinia hordei</i>	R to S	R	Rubiales unpubl.
<i>Puccinia graminis</i> f.sp. <i>tritici</i>	R to S	R to S	Rubiales et al. 1993a, c
<i>Blumeria graminis</i> f.sp. <i>tritici</i>	R	R to S	Rubiales et al. 1993a
<i>Blumeria graminis</i> f.sp. <i>hordei</i>	R	R	Rubiales et al. 1993c
<i>Blumeria graminis</i> f.sp. <i>secalis</i>	R	R	Rubiales et al. 1992a
<i>Mycosphaerella graminis</i>	R	R to S	Rubiales et al. 1996a
<i>Phaeosphaeria nodorum</i>	MR	MR to S	Rubiales et al. 1996a
<i>Fusarium culmorum</i>	MR to S	MR to S	Rubiales et al. 1996a
<i>Ustilago tritici</i>	R	R to S	Nielsen 1987, Rubiales unpubl.
<i>Ustilago nuda</i>	R	R	Nielsen 1987, Rubiales unpubl.
<i>Tilletia indica</i>	R	S	Chauhan and Singh 1997
<i>Tilletia caries</i>	R	R	Rubiales et al. 1996
<i>Pyrenophora tritici-repentis</i>	MR	R <sup>2</sup> to S	Sillero and Rubiales unpubl.
<i>Pyrenophora teres</i>	R to MR	R to S	Rubiales, unpubl.
<i>Rhynchosporium secalis</i>	R to MR	R	Rubiales, unpubl.
<i>Pseudocercospora herpotrichoides</i>	R to S	R to S	Rubiales, unpubl.
<i>Gaeumannomyces graminis</i>	MR to MS	-	Jorgensen and Jensen 1976
<i>Diuraphis noxia</i>	R	-	Clement and Lester 1990
<i>Schizaphis graminum</i>	R to S	-	Castro et al. 1994
<i>Meloidogyne naasi</i>	R	S	Person-Dedryver et al. 1990
<i>Meloidogyne chitwoodi</i>	R	-	Jensen and Griffin 1994
<i>Heterodera avenae</i>	S	S	Rubiales and Paetz, unpubl.
<i>Mayetiola destructor</i>	R to S	R to S	Rubiales and del Moral unpubl.

<sup>a</sup> Reaction of the wheat lines used as parents of tritordeums, other wheat lines may exist with different reaction.

<sup>b</sup> The reaction of the tritordeum was that of their respective wheat parental lines, whatever the resistance or susceptibility of their *H. chilense* parents.

<sup>c</sup> The infection type of tritordeum lines was that of their wheat parental lines, but there was a quantitative contribution of the resistance of *H. chilense* resulting in a reduction in the infection frequency in tritordeum.

<sup>d</sup> Resistance of tritordeum diluted at higher ploidy levels. All hexaploid tritordeums studied were immune, but some susceptibility was displayed by the octoploid tritordeums with a susceptible wheat parent.

<sup>e</sup> Some tritordeums were more resistant than their wheat parents, others were not.

was highly resistant (HT8) but the other two were highly susceptible (HT9 and HT28). It was suggested that resistance is under simple genetic control and that it had been retained or lost by chance during selection made in the absence of Karnal bunt infection pressure. This suggestion requires verification but raises an important point. All other studies of disease resistance in tritordeum have employed primary tritordeums, i.e. amphiploids obtained after chromosome doubling of the hybrids, without further breeding. By contrast, the study of resistance to Karnal bunt, involving secondary tritordeums coming from selections of crosses among hexaploid and octoploid tritordeums, allowed CHAUHAN and SINGH (1997) to propose simple genetic control of resistance. This conclusion requires substantiation, but more extensive use of secondary lines may provide evidence for whether resistance to the various pathogens is under simple or complex genetic control.

*H. chilense* is resistant to loose smuts of wheat and barley (*Ustilago tritici* and *U. nuda*, respectively) (NIELSEN 1987). There is a quantitative contribution of the resistance in tritordeum (D. Rubiales, unpubl.) (Table 6).

#### Resistance to *Fusariosis*

*H. chilense* is slightly susceptible to *Fusarium culmorum*. Tritordeum as a crop can also be regarded as being susceptible, but some tritordeums are more resistant than their wheat parent (RUBIALES et al. 1996a) (Table 6). Measurement of the content of ergosterol (to estimate fungal biomass) and of the phytotoxic mycotoxin deoxinivalenol showed that the level of resistance to colonisation by *Fusarium* is on average higher in tritordeum than in wheat. Some *H. chilense* genotypes (H7, H17, H56, H61) enhanced resistance to *F. culmorum* in tritordeum hybrids, while others (H1, H11, H12, H13) did not. As there does not seem to be specialisation for resistance to *F. culmorum*, *F. graminearum* or *F. nivale*, it is anticipated that the resistance of particular tritordeum lines will be effective against all three fungi. This suggestion is supported by preliminary data on the reaction of a few tritordeum lines to *F. graminearum* (G. Fedak, pers. comm.).

#### Resistance to other pathogens

*H. chilense* is moderately resistant to tan spot of wheat incited by *Pyrenophora tritici-repentis* (anamorph *Drechslera tritici-repentis*) (D. Rubiales, unpubl.). This resistance is expressed in tritordeum with a quantitative reduction of infection (Table 6).

*H. chilense* is resistant to net blotch incited by *P. teres* (anamorph *D. teres*) and to scald (*Rhynchosporium secalis*) (Table 1). This might be useful in barley

and rye breeding. Tritordeum is resistant to these diseases.

*H. chilense* is moderately susceptible to take-all (*Gaeumannomyces graminis*) (JORGENSEN and JENSEN 1976), and so is tritordeum (Table 6) and the four addition lines in wheat that have been studied so far (HOLLINS and SCOTT 1986).

*H. chilense* and tritordeum are susceptible to *Pseudocercospora herpotrichoides* (D. Rubiales, unpubl.) (Table 6).

#### Resistance to nematodes and aphids

*H. chilense* is resistant to the Columbia root-knot nematode (*Meloidogyne chitwoodi*) (JENSEN and GRIFFIN 1994) and to the root-knot nematode (*M. naasi*) (PERSON-DEDRYVER et al. 1990) but is susceptible to *Heterodera avenae* (D. Rubiales and Paez, unpubl.). Although *M. naasi* was able to form galls, resistance severely limited the number of nematodes that could establish within roots and reduced their reproduction. The resistance factor was located on the short arm of chromosome 1H<sup>ch</sup>. There was a gene dose effect, the expression of resistance being slightly higher in plants disomic for 1H<sup>ch</sup> than in monosomics. Resistance was reduced at the octoploid level in the only 8 × tritordeum studied.

Levels of resistance to greenbug (*Schizaphis graminum*) have been reported to vary between *H. chilense* lines (CASTRO et al. 1994). Antixenosis, antibiosis and tolerance mechanisms were detected. Different plant characters appeared to prolong aphid developmental time and reduce the length of adult life and total fecundity. Genes with positive effects on antixenosis were located on chromosome 1H<sup>ch</sup>, genes for prolonged aphid developmental time on chromosomes 5H<sup>ch</sup> and 7H<sup>ch</sup>, genes for reduction of total fecundity on 4H<sup>ch</sup>, and genes for host tolerance on 7H<sup>ch</sup> (CASTRO et al. 1996).

*H. chilense* is also known to possess resistance to the aphids *Diuraphis noxia* (CLEMENT and LESTER 1990) and *Rhopalosiphum padi* (WEIBULL 1987). However, it possesses little resistance to Hessian fly (*Mayetiola destructor*) (D. Rubiales and Del Moral, unpubl.)

#### Conclusion

*H. chilense* appears to offer a valuable reservoir of genes for disease resistance that potentially can be exploited in cereal breeding. Feasibility for transference of traits from *H. chilense* to cereals has been previously discussed (MARTÍN et al. 1996, 1998, 2000).

Some of the resistances described in *H. chilense* seem to be under complex genetic control with influential factors present on several chromosomes. The

use of such broadly based resistance is most desirable in breeding for resistance as is likely to be more durable than simply-controlled resistance. However, it will be difficult to transfer simultaneously multiple genetic factors governing different resistance mechanisms to an agronomically valuable cultivar. Nevertheless, even the transfer of a single factor conveying novel resistance could be of value.

Mechanisms in *H. chilense* that lead to avoidance of attack by rusts and resistance mechanisms that prevent haustorium formation by rusts and mildews are particularly interesting. These may provide novel forms or sources of resistance which can be transferred to germplasm of major commercial cereal species. They could be used either alone or in combination with genes conditioning hypersensitive resistance to add complexity to plant defences thereby adding to the durability of crop protection.

#### ACKNOWLEDGEMENTS

We are gratefully indebted to the CICYT projects AGF96-0463 and AGF99-1036 for the financial support and to A. Moral, C. Martínez and M.C. Ramírez for technical assistance

#### REFERENCES

- Castro AM, Martín A and Martín LM, (1996). Location of genes controlling resistance to greenbug (*Schizaphis graminum* Rond.) in *Hordeum chilense*. *Plant Breed.* 115: 335–338.
- Castro AM, Martín LM, Martín A, Arriaga HO, Tobes N and Almaraz LB, (1994). Screening for greenbug resistance in *Hordeum chilense* Roem et Schult. *Plant Breed.* 112: 151–159.
- Chauhan RS and Singh BM, (1997). Resistance to Karnal bunt in *Hordeum chilense* and its amphiploids with *Triticum* species. *Euphytica* 96: 327–330.
- Clement SL and Lester DG, (1990). Screening wild *Hordeum* species for resistance to Russian wheat aphid. *Cereal Res. Comm.* 18: 173–177.
- Fedak G, (1992). Intergeneric hybrids with *Hordeum*. In: *Barley: Genetics, Biochemistry, Molecular Biology and Biotechnology* (ed. PR Shewry). CAB International, UK, p. 45–70.
- Hollins TW and Scott PR, (1986). Take-all. In: *Plant Breeding Institute Annual Report 1986*. UK, p. 102–103.
- Jensen KB and Griffin GD, (1994). Resistance of diploid *Triticeae* species and accessions to the Columbia root-knot nematode *Meloidogyne chitwoodi*. *J. Nematol.* 26: 635–639.
- Jorgensen JH and Jensen HP, (1976). Screening of *Hordeum* species for resistance to the take-all fungus, *Gaeumannomyces graminis*. *Z. Pflanzzüchtg.* 76: 200–203.
- Kerber ER, (1991). Stem rust resistance in 'Canthatch' hexaploid wheat induced by a nonsuppressor mutation on chromosome 7DL. *Genome* 34: 935–939.
- Kruse A, (1973). *Hordeum* × *Triticum* hybrids. *Hereditas* 73: 157–161.
- Martín A and Cubero JI, (1981). The use of *Hordeum chilense* in cereal breeding. *Cereal Res. Comm.* 9: 317–323.
- Martín A, Cabrera A, Hernández P, Ramírez MC and Rubiales D, (2000). Prospects for the use of *Hordeum chilense* in durum wheat breeding. *Options Méditerranéennes* 40: 111–115.
- Martín A, Martín LM, Cabrera A, Ramírez MC, Jiménez MJ, Rubiales D, Hernández P and Ballesteros J, (1998). The potential of *Hordeum chilense* in breeding *Triticeae* species. In: *Triticeae III* (ed. AA Jaradat). Science Publisher, Inc, USA, p. 377–386.
- Martín A, Martínez-Araque C, Rubiales D and Ballesteros J, (1996). Tritordeum: triticales' new brother cereal. In: *Triticale: Present and Future* (eds H Guades-Pinto et al.). Kluwer Academic Publishers, Dordrecht, p. 57–72.
- McNeal FH, Konzak CF, Smith EP, Tate WS and Russel TS, (1971). A uniform system for recording and processing cereal research data. USDA, ARS Publication, p. 34–121.
- Nielsen J, (1987). Reaction of *Hordeum* species to the smut fungi *Ustilago nuda* and *U. tritici*. *Can. J. Bot.* 65: 2024–2027.
- Person-Dedryver F, Jahier J and Miller TE, (1990). Assessing the resistance to cereal root-knot nematode, *Meloidogyne naasi* in a wheat line with the added chromosome arm 1HchS of *Hordeum chilense*. *J. Genet. Breed.* 44: 291–296.
- Rubiales D and Carver TWL, (2000). Cellular responses of *Hordeum chilense* genotypes to inappropriate formae specialis of the cereals powdery mildew fungus. *Can. J. Bot.* 78: 1561–1570.
- Rubiales D and Martín A, (1999). Chromosomal location in *Hordeum chilense* of resistance to common bunt. *Euphytica* 109: 157–159.
- Rubiales D and Niks RE, (1992a). Low appressorium formation by rust fungi on *Hordeum chilense* lines. *Phytopathology* 82: 1007–1012.
- Rubiales D and Niks RE, (1992b). Histological responses in *Hordeum chilense* to brown and yellow rust fungi. *Plant Pathol.* 41: 611–617.
- Rubiales D and Niks RE, (1996). Avoidance of rust infection by some genotypes of *Hordeum chilense* due to their relative inability to induce the formation of appressoria. *Physiol. Mol. Pl. Pathol.* 49: 89–101.
- Rubiales D, Ballesteros J and Martín A, (1991). The reaction of X Tritordeum and its *Triticum* spp. and *Hordeum chilense* parents to rust diseases. *Euphytica* 54: 75–81.
- Rubiales D, Ballesteros J and Martín A, (1992a). Resistance to *Septoria tritici* in *Hordeum chilense* × *Triticum* spp. Amphiploids. *Plant Breed.* 108: 281–286.
- Rubiales D, Ramírez MC and Niks RE, (1992b). The contribution of *Hordeum chilense* to partial resistance of Tritordeum to wheat brown rust. *Euphytica* 59: 129–133.
- Rubiales D, Brown JKM and Martín A, (1993a). *Hordeum chilense* resistance to powdery mildew and its potential use in cereal breeding. *Euphytica* 67: 215–220.
- Rubiales D, Niks RE, Dekens RG and Martín A, (1993b). Histology of the infection of tritordeum and its parents by cereal brown rust. *Plant Pathol.* 42: 93–99.



- Rubiales D, Niks RE and Martín A, (1993c). Genomic interactions in the resistance to mildew and rust fungi in hybrids and amphiploids involving the genera *Triticum*, *Hordeum* and *Secale*. *Cereal Res. Comm.* 21: 187–194.
- Rubiales D, Nicholson P, Snijders CHA and Martín A, (1996a). Reaction of tritordeum to *Septoria nodorum* and *Fusarium culmorum*. *Euphytica* 88: 165–174.
- Rubiales D, Ramírez MC and Martín A, (1996b). Resistance to common bunt in *Hordeum chilense* × *Triticum* spp. Amphiploids. *Plant Breed.* 115: 416–418.
- Rubiales D, Ramírez MC and Niks RE, (1996c). Avoidance to leaf rust fungi in wild relatives of cultivated cereals. *Euphytica* 87: 1–6.
- Rubiales D, Reader SM and Martín A, (2000). Chromosomal location of resistance to *Septoria tritici* in *Hordeum chilense* determined by the study of chromosomal addition and substitution lines in ‘Chinese Spring’ wheat. *Euphytica* 115: 221–224.
- Rubiales D, Carver TWL and Martín A, (2001). Expression of resistance to *Blumeria graminis* f.sp. *tritici* in ‘Chinese Spring’ wheat addition lines containing chromosomes from *Hordeum vulgare* and *H. chilense*. *Hereditas* 134: 53–57.
- Rubiales D, Ramírez MC, Carver TLW and Niks RE, (2002). Abnormal germling development by brown rust and powdery mildew confers disease avoidance to cereals mutants. *Hereditas* 135: 000–000.
- Vaz Patto MC, (2001). The genetics and mechanism of avoidance of rust infection in *Hordeum chilense*. PhD thesis, Wageningen Agric. Univ.
- Vaz Patto MC, Aardse A, Buntjer J, Rubiales D, Martín A and Niks RE, (2001). Morphology and AFLP markers suggest three *Hordeum chilense* ecotypes that differ in avoidance to rust fungi. *Can. J. Bot.* 79: 204–213.
- Vaz Patto MC and Niks RE, (2001). Leaf wax layer may prevent appressorium differentiation but does not influence orientation of the leaf rust fungus *Puccinia hordei* on *Hordeum chilense* leaves. *Europ. J. Plant Pathol.* 107: 795–803.
- Weibull J, (1987). Screening for resistance against *Rhopalosiphum padi* (L): *Hordeum* species and interspecific hybrids. *Euphytica* 36: 571–575.