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POWDERY MILDEW RESISTANCE IN RECOMBINANT LINES
ORIGINATING FROM CROSSES BETWEEN *HORDEUM*
VULGARE AND *HORDEUM BULBOSUM*

ABSTRACT

Six recombinant lines obtained from crosses and backcrosses of barley cultivars (backcrossing parents) and accessions of *H. bulbosum* were tested with 18 differential isolates of *Blumeria graminis* f.sp. *hordei*. Based on screening tests it was concluded that resistance to powdery mildew is present in all tested recombinant lines. Outstanding resistance to powdery mildew was identified in line 81882/83/3/2/9. This line showed resistance reaction 2 for inoculation with all isolates used. In 2 lines (81882/83/3/2/9 and 4176/n/3/2/6) it was not possible to postulate presence of known resistance genes for powdery mildew resistance. However based on fact that these lines comes from cross of cultivar Vada which expresses very limited resistance to powdery mildew with accession S1 (*H. bulbosum*) it may be concluded that expressed resistance comes from *H. bulbosum*. Moreover we can postulate presence in line 81882/83/3/2/9 of gene or genes which determine resistance reaction 2 for powdery mildew. In 4 other lines originating from cross of cultivar Emir and *H. bulbosum* the presence of unknown genes together with *Mla12* was postulated. Most probably gene *Mla12* postulated to be present in these lines originate from barley cultivar Emir and unknown gene or genes postulated originate from *H. bulbosum* parents. The possibilities to use hybrid lines with identified resistance to powdery mildew originating from *H. bulbosum*, especially line 81882/83/3/2/9 resistant to infection with all isolates used, in barley breeding programmes were discussed.

Key words: *Hordeum bulbosum*, powdery mildew, *Blumeria graminis* f.sp. *hordei*, recombinant lines, resistance genes

INTRODUCTION

Barley (*Hordeum vulgare* L.) is the fourth most important cereal crop in the World and in many regions of the world in which it is the most important crop. In North Africa, Central Asia and South America barley is grown in places where other cereals are not suitable for farming due to harsh environmental conditions such as high altitude, low rainfall (<300 mm annually), or soil salinity (Bothmer *et al.*, 1995, 2003a; Fischbeck, 2003; Czembor, 1996, 2005) and is often attacked by barley powdery mildew fungus (*Erysiphe graminis* DC. f. sp. *hordei* Em Marchal - synonym *Blumeria*

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graminis DC. Golovin ex Speer f. sp. *hordei*). The primary loss from powdery mildew is reduced yield, which can reach up to 20% - 30% (Lim and Gaunt, 1986; Ceccarelli *et al.*, 1995; Jørgensen, 1994; Zine Elabidine, 1992). In addition to yield losses powdery mildew infection results in lowering of quality characteristics. This is especially detrimental for malting barley (Griffiths, 1984; Balkema-Boomstra and Masterbroek, 1995).

Powdery mildew on barley is considered as one of the most clearly characterized system of host-pathogen genetic interactions. Since 1907, when Biffen started genetic studies of barley resistance to powdery mildew, in barley more than 100 mildew resistance loci have been identified. In Europe, the use of specific resistance genes to control barley powdery mildew began in the 1930s with the work of Honecker which was stimulated by an extraordinarily heavy attack of this pathogen in Germany in 1929 (Biffen, 1907; 1991; Honecker, 1938; Jørgensen, 1994; Czembor, 2005). Since that period, barley cultivars with effective genes for resistance to major pathogens has been an efficient means for controlling major diseases and preventing yield losses (Czembor, 1996, 2005; Fischbeck, 2003; Weibull *et al.*, 2003). Barley breeders commonly used such resistance genes as *Mla6*, *Mla7*, *Mla9*, *Mla12* and *Mla13* belonging to the *Mla* locus and the resistance alleles *Mlk*, *Mlg*, *MLLa*, *Mlh* and *Mlra*. However, virtually all of these genes were gradually overcome by virulent races within 4-5 years when cultivars containing them were used on a large acreage (Munk *et al.*, 1991; Jørgensen, 1994; Czembor and Czembor, 1998, 1999b) Because of this fact, barley breeders, geneticists and plant pathologists are looking for new efficient sources of resistance to powdery mildew to combine them with already used in modern cultivars in order to increase the resistance durability (Honecker, 1938; Ralski and Mikołajewicz, 1958; Nover and Lehmann, 1973; Wiberg, 1974; Czembor *et al.*, 1979; Czembor, 1976, 1996, 2005; Negassa, 1985; Lehmann and von Bothmer, 1988; Leur *et al.*, 1989; Leijerstam, 1996; Jørgensen and Jensen, 1997; Lehmann *et al.*, 1998; Czembor and Czembor, 1999a; Czembor and Johnston, 1999; Jönsson and Lehmann, 1999; Czembor and Frese, 2003; Bonman *et al.*, 2005; Shtaya *et al.*, 2006c).

Barley gene pool can be divided in three parts (Bothmer *et al.*, 1995; 2003b). In the primary gene pool of barley are *H. spontaneum* and *H. vulgare* (Nevo, 1985). *H. spontaneum* was used successfully in many breeding programmes to transfer of new disease resistances and tolerance to abiotic stress (Lehmann, 1991; Brian *et al.*, 1995; Eglinton *et al.*, 1999; Fischbeck, 2003; Backes *et al.*, 2003; Pickering and Johnston, 2005). In the secondary gene pool of barley is only one species which is bulbous barley grass (*H. bulbosum* L.) (Pickering *et al.*, 1999, 2004b; Bothmer *et al.*, 2003b; Pickering and Johnston, 2005). It is perennial and occurs in the Mediterranean region, West Asia, Caucasus Mountains and part of Central Asia including Iran, Afganistan, Turkmenistan, Uzbekistan, Kazakhstan. It

occurs as both diploid and autotetraploid cytotypes. It normally requires vernalisation to flower and has a strong self-incompatibility system based on two loci (Lundqvist, 1962; Bothmer *et al.*, 1995). In the tertiary gene pool of barley are 29 *Hordeum* species. These species are diploid, tetraploid and hexaploid forms and they are found in North and South America, Europe, the Middle East, Central Asia and South Africa (Bothmer *et al.*, 1995). In some breeding programmes attempts have been made to use these species in crosses with *H. vulgare* but with very limited success (Bothmer *et al.*, 1995, 2003; Pickering and Johnston, 2005).

Bulbous barley grass during last 40 years has been used mainly to obtain doubled haploids (Kasha and Kao, 1970; Pickering and Johnston, 2005). Over years this technique was much improved and now the interspecific cross is often used in conjunction with androgenesis to obtain a reliable source of haploids (Pickering and Devaux, 1992; Pickering *et al.*, 1999). *H. bulbosum* was described as species with very high level of resistance to barley pathogens including powdery mildew (Xu and Snape, 1989; Zeller, 1998; Pickering *et al.*, 2004b; Pickering and Johnston, 2005). Despite of these observations, the number reports on genetic investigations on *H. bulbosum* and on successful transfer of resistance to major pathogens from *H. bulbosum* to *H. vulgare* is very limited (Pohler and Szigat, 1982; Szigat and Szigat, 1991; Zhang *et al.*, 2001; Pickering and Johnston, 2005). In these reports hybrid lines of *H. bulbosum* × *H. vulgare* expressed resistance to such diseases as leaf rust, powdery mildew, scald, septoria speckled leaf blotch, BaYMV/BaMMV and stem rust (Pickering *et al.*, 1987, 1995, 2000a, 2006b; Xu and Snape, 1989, Xu and Kasha, 1992, Michel *et al.*, 1994, Steffenson, 1998, 1999; Walther *et al.*, 2000; Ruge *et al.*, 2003, 2005; Fetch *et al.*, 2004, Shtaya, 2007).

Major obstacle for limited use of *H. bulbosum* as source of resistance in barley breeding programmes are pre and post fertilisation interspecific crossability barriers. These barriers include: pollen tube-stylar incompatibility, endosperm degeneration, chromosome instability, low chromosome pairing and certation effects (Kasha and Kao, 1970, Pickering and Hayes, 1976; Pickering, 1980; Xu and Snape, 1988; Thörn, 1992a, 1992b; Zhang *et al.*, 1999, 2002; Pickering *et al.*, 2005). Some of these barriers can be solved by careful selection of parental genotype and the environment in which to carry out crosses (Pickering, 1981, 1983, 1984, 1994; Thomas and Pickering, 1985; Pickering and Rennie, 1990; Pickering *et al.*, 2004a, 2004b, 2006a). Pickering and his co-workers described hybrids *H. vulgare* × *H. bulbosum* and their backcrossing to *H. vulgare* (Pickering, 1987, 1988; Pickering *et al.*, 1994, 1995, 2000a, 2000b). Several of the recombinant lines showed improved resistance to major pathogens of barley including leaf rust (Pickering *et al.*, 1995, 2000a; Pickering, 2000).

The objective of this study was to investigate powdery mildew resistance in recombinant lines obtained from crosses between *H. bulbosum* and *H. vulgare*.

MATERIALS AND METHODS

Plant material

Six recombinant lines obtained from crosses and backcrosses of barley cultivars (backcrossing parents) and accessions of *H. bulbosum* were tested (Table 1). In addition 2 cultivars (Emir and Vada) which were backcrossing parents for specific recombinant lines were tested. Recombinant lines were obtained at New Zealand Institute for Crop and Food Research, New Zealand (Pickering 1987, 1988; Pickering *et al.*, 1987, 1998, 2000a). In progeny of line 172N2 albinos plants were present.

Table 1
Recombinant lines, their pedigrees and chromosome location of *H. bulbosum* introgression

Lp.	Line	<i>H. vulgare</i> parent	<i>H. bulbosum</i> parent	Chromosome location of <i>H. bulbosum</i> introgression
1	81882/83/3/2/9	Vada	S1	2HS
2	4176/n/3/2/6	Vada	S1	
3	38P18/5-13/1-9	Emir	HB2032	2HL
4	102C2/18	Emir	HB2032	2HL
5	120G5a/17	Emir	Cb 2920/4 × Cb 2929/1)	6HS (+7HS?)
6	172N1	Emir	Cb 2920/4 × Cb 2929/1)	6HS (+7HS?)

Pathogen

Eighteen isolates of *B. graminis* f. sp. *hordei* Em Marschal were used (Table 2). They originated from the collections in Risø National Laboratory, Roskilde, Denmark; Danish Institute for Plant and Soil Science, Lyngby, Denmark; Edigenossische Technische Hochschule – ETH, Zurich, Switzerland provided kindly by Dr. H. J. Schaerer (ETH, Zurich, Switzerland) and IHAR Radzików, Poland. The isolates were chosen according to differences in virulence spectra that were observed on the Pallas isolines differential set (Kølster *et al.*, 1986), provided by Dr. L. Munk (Royal Agricultural and Veterinary University, Copenhagen, Denmark). They were purified by single pustule isolation and were maintained and propagated on young seedlings of the powdery mildew susceptible cultivar Manchuria (CI 2330). Frequent virulence checks were made to assure the purity of isolates throughout the experiment.

Table 2
Differential isolates and their infection types on differential set.

No.	Lines and cultivars	Isolates																
		1	2	8	11	13	14	24	28	29	31	36	39	40	48	50	51	57
1.	Pallas (a8)	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4	4
2.	P01 (a1)	0	0	4	0	0	0	0	0	4	0	4	0	0	0	0	4	0
3.	P02 (a3)	0	0	0	0	0	0	0	0	0	0	0	0	4	0	4	0	0
4.	P03 (a6,a14)	0	0	0	4	0	0	2	4	0	0	4	0	4	4	4	4	4
5.	P04A (a7,lk)	4	4	0	2	2	2	0	0	4	4	4	4	2	0	2	2	4
6.	P04B (a7,+?)	4	4	1	2	4	4	0	1	4	4	4	4	2	0	2	4	4
7.	P06 (a7,LG2)	4	4	0	0	4	4	0	0	4	4	4	4	2	0	2	2	4
8.	P07 (a9,lk)	4	0	0	0	4	0	0	0	4	0	0	0	0	0	0	0	4
9.	P08A (a9,lk)	4	0	0	0	4	0	0	0	4	0	0	0	0	0	0	0	4
10.	P08B (a9)	4	0	0	0	4	0	4	0	4	0	0	0	0	0	0	0	4
11.	P09 (a10,Du2)	4	4	0	0	4	0	0	0	4	4	4	2	0	0	4	4	4
12.	P10 (a12)	0	0	0	0	0	4	0	0	4	4	4	0	4	0	4	4	0
13.	P11 (a13,Ru3)	4	0	0	0	0	4	0	0	4	4	0	0	0	0	0	4	4
14.	P12 (a22)	4	4	4	4	0	4	4	4	0	4	0	4	4	4	0	4	0
15.	P13 (a23)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
16.	P14 (ra)	4	4	4	4	4	0	4	4	4	4	4	4	4	4	4	4	4
17.	P15 (Ru2)	2	2	2	4	4	2	2	4	4	4	4	4	4	4	2	4	4
18.	P17 (k)	4	4	2	2	4	2	2	2	4	4	4	4	2	2	4	4	4

Disease Assessment

After 8 – 10 days of incubation, the infection types were scored according to a 0 – 4 scale developed by Mains and Dietz (1930) (Table 3). The seedlings were classified into susceptible or resistant groups. Plants scored 0 – 2 were included into resistant group and plants scored 3 and 4 were included in the susceptible group.

Description of infection types and codes used (Mains and Dietz, 1930).

Table 3

Infection type	Macroscopic symptoms
0	No visible symptoms. (Immunity).
1	Necrotic flecks, usually minute. Chlorosis often present. No mycelial growth. No sporulation. (Hypersensitivity).
2	Necrotic flecks, often with chlorosis. Reduced mycelial growth. No or scarce sporulation.
3	Necrotic flecks or small necrotic areas. Frequent chlorosis. Moderate mycelial growth, moderate sporulation.
4	Profuse sporulation of well developed colonies and sometimes green islands.

Resistance tests

From five to ten plants per each recombinant line were tested with 18 isolates of powdery mildew (Table 4). Testings was conducted in the IHAR Radzików greenhouse. The plants were grown with 16 h lights and 16-22°C range of temperature. The inoculation was carried out when plants were 10 – 12 days old (2 leaf stage) by shaking or brushing conidia from diseased plants. After 8-10 days of incubation the disease reaction types showed by seedlings were scored.

Postulation of resistance alleles

Hypotheses about the specific resistance genes present were made from the comparison of the reaction spectra of the tested lines with those of differential lines. Identification of resistance genes was made by eliminating resistance genes not present in tested lines. Next step was determining the postulated and possible resistance genes. It was done on the basis of the gene for gene hypothesis (Flor, 1956).

RESULTS

All 6 lines tested possessed resistance to powdery mildew. Line 81882/83/3/2/9 was resistant to infection with all isolates used and tested plants expressed resistant reaction 2 for infection with all isolates. In this line and line 4176/n/3/2/6 the presence of unknown gene or genes for resistance was postulated. In 4 other lines (38P18/5-13/1-9, 102C2/18, 120G5a/17 and

Table 4
Reaction of 6 recombinant lines and 2 cultivars to infection with 18 isolates of *PBlumeria graminis* f.sp. *hordei*.

No.	Lines / cultivars	Isolates																		Postulated genes
		1	2	8	11	13	14	24	28	29	31	36	39	40	48	50	51	57	63	
1	81882/83/3/2/9	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	?	
2	4176/m/3/2/6	2	4	4	2	4	4	0&*4	4	4	4	4	4	4	2	4	4	4	?	
3	38P18/5-13/1-9	1	1	1	0	0	4	1	0	4	4	4	0	4	2	4	4	2	Mla12, ?	
4	102C2/18	1	1	2	0	0	4	1	0	4	4	4	0	4	2	4	4	2	Mla12, ?	
5	120GA/17	0	0	1	0	0	2	1	0	4	4	4	0	4	1	4	4	1	Mla12, ?	
6	172N2	0	0	1	0	0	2	1	0	4	4	4	0	4	1	4	4	1	Mla12, ?	
	Emir	0	1	0	0	0	4	0	0	4	4	0	4	0	4	4	0	4	Mla12	
	Vada	4	2	4	4	2	4	4	4	4	4	4	4	4	4	4	4	4	?	

* & - segregation of resistance reaction (e.g. 0 & 4 means that some plants had 0 resistance reaction and another 4)

172N1) the presence of unknown genes for resistance together with gene *Mla12* was postulated. In one line 4176/n/3/2/6 heterogenous resistance reactions (0 and 4) were expressed after inoculation with one isolate of powdery mildew.

DISCUSSION

Wild relatives of the cultivated crop plant including barley can be used as source of useful characteristics for breeding. These characteristics include resistance to biotic and abiotic stresses (Pickering *et al.*, 1987, 1995, 2000a; Xu and Kasha, 1992; Michel *et al.*, 1994; Walther *et al.*, 2000; Thomas, 2003; Ruge *et al.*, 2003). Currently, powdery mildew of barley is one of the most common and most widespread disease of barley causing significant yield losses. However, this disease opposite to leaf rust was, for a long time, not important factor in barley production. In Europe the first devastating epidemic of barley powdery mildew was observed in Germany on winter barley in 1901 and on spring barley in 1903 (Wolfe and Schwarzbach, 1978). Most probably it happened because modern agricultural methods were introduced by German farmers. These methods included the use high crop densities, the application of nitrogen fertilizers and on the large scale cultivation of uniform varieties (Wolfe and Schwarzbach, 1978; Wolfe, 1984).

However breeding for resistance to powdery mildew of barley is faced with a highly mobile pathogen, whose gene-pool forms an almost infinite source of genetic variation (Müller *et al.*, 1996; Limpert *et al.*, 1999, 2000; Czembor and Czembor, 2004). A number of genes for specific resistance have been used in commercial barley varieties since the first gene, *Mlg*, was introduced on a large scale in the 1930s in Germany (Wolfe and Schwarzbach, 1978; Jørgensen, 1994; Wolfe and MacDermott, 1994). In this century in Europe more than 700 cultivars of barley have been used with different combinations of 36 alleles for race-specific resistance to powdery mildew. However, 28 of these alleles are closely linked or allelic, which limits the possible number of gene combinations in breeding of new varieties (Brown and Jørgensen, 1991; Jørgensen, 1994; Wolfe and McDermott, 1994). Almost all of these genes were successively overcome by the appearance of pathotypes with matching virulence. These varieties had to be discarded because they were the far too disease susceptible to be of any further value. This susceptibility was mainly due to a host erosion of partial resistance during breeding for race-specific resistance (*Vertifolia effect*) (Wolfe and Schwarzbach, 1978; Jørgensen, 1994; Wolfe and MacDermott, 1994).

Presented study confirmed findings of other investigators that hybrid lines of *H. bulbosum* x *H. vulgare* possess resistance to major pathogens of barley including powdery mildew (Pickering *et al.*, 1987, 1995, 2000a, 2006b; Xu and Kasha, 1992; Michel *et al.*, 1994; Pickering *et al.*, 1999, 2004b; Walther *et al.*, 2000; Ruge *et al.*, 2003; Pickering and Johnston, 2005; Shtaya *et al.*, 2007).

Based on screening tests it may be concluded that resistance to powdery mildew is present in all tested recombinant lines. Outstanding resistance to powdery mildew was identified in line 81882/83/3/2/9. This line showed resistance reaction 2 for inoculation with all isolates used. In 2 lines (81882/83/3/2/9 and 4176/n/3/2/6) it was not possible to postulate presence of known resistance genes for powdery mildew resistance. However based on fact that these lines comes from cross of cultivar Vada (with very limited resistance to powdery mildew) with accession S1 (*H. bulbosum*) it may be concluded that expressed resistance comes from *H. bulbosum*. Moreover we can postulate presence in line 81882/83/3/2/9 of gene or genes which determine resistance reaction 2 for powdery mildew. In 4 other lines originating from cross of cultivar Emir and *H. bulbosum* the presence of unknown genes together with *Mla12* was postulated. Most probably gene *Mla12* postulated to be present in these lines originate from barley cultivar Emir and unknown gene or genes originate from *H. bulbosum* parents.

In presented study seedling resistance tests were used in order to describe infection types expressed by barley plants after inoculation with differential isolates of powdery mildew. This kind of testing as sufficient for screening for disease resistance and it is used commonly in many breeding programs to postulate the presence of specific genes for resistance in modern cultivars and to screen for new sources of effective resistance (Parlevliet, 1976; Jin *et al.*, 1995; Brooks *et al.*, 2000; Shtaya *et al.*, 2006b; Czembor and Czembor, 2007a, 2007b; Czembor and Bladenopoulos, 2007). However, by using this kind of tests it is not possible or at least it is difficult to identify and describe partial resistance. For description of this kind of resistance we need conduct additional to infection type measurements of characteristics for this kind of resistance. In addition, partial resistance is generally better expressed at the adult plant stage (Parlevliet and van Ommeren, 1975; Smit and Parlevliet, 1990; Martinez *et al.*, 2001; Shtaya *et al.*, 2006a; Ochoa and Parlevliet, 2007). It will be very interesting if further studies of described hybrid lines will also include parameters describing partial resistance and extension of resistance studies to plants at adult stage. Final determination of the number of resistance genes and the type of their action in tested hybrid lines may be established by crosses and backcrosses among appropriate genotypes (Jin and Steffenson, 1994; Czembor, 1996, 2005; Czembor and Czembor, 2001; Czembor *et al.*, 2006).

The durability of the resistance genes to powdery mildew present in barley cultivars may be increased by using many different strategies for deploying resistance genes (Parlevliet, 1983; Wolfe, 1984, 1993; Finckh *et al.*, 1996, 1999, 2000). These strategies are: combining partial (minor genes) and race-specific (major) resistance genes, multiline cultivars, partial resistance, combining different race-specific resistance genes into one cultivar and deploying many cultivars with different resistance genes in space (e.g. cultivar mixtures) or time (winter versus spring barley) (Parlevliet, 1983; Finckh *et al.*, 2000; Brown and Hovmřller, 2002; McDonald and Linde, 2002). Very important for dura-

bility of resistance to powdery mildew in agricultural practice is proper use of new sources of resistance to this pathogen including those described in this paper (Brown and Hovmüller, 2002; McDonald and Linde, 2002; Czembor, 2005).

Many scientists expressed view that genetic base of cultivated varieties is limited and that breeders are restricted to crossing within the primary gene pool, which consists of *H. vulgare* (in form of modern cultivars and landraces) and its closest diploid relative, *H. spontaneum* (Czembor, 1996, 2005; Russell *et al.*, 2000; Pickering and Johnston, 2005). However presented study showed that secondary barley gene pool can be source of very valuable characteristics for barley breeding. Broadening of genetic base of cultivated barley varieties and description of new sources of resistance are also important because future strategies for the control of barley pathogens will have to focus increasingly on more ecologically acceptable pest control methods. Any usage of chemicals (pesticides, fungicides, herbicides, and mineral fertilizers) in agriculture is increasingly criticized in societies of many countries. Breeding for resistance represent such ecologically safe method. In addition to ecological also economical arguments (use of fuel, labour, special machines) and development of fungicide resistance in population of powdery mildew are in favour of breeding for resistance versus chemical control (Gullino and Kuijpers, 1994; Brown, 1996; Nierobca *et al.*, 2003). Hybrid lines with identified resistance to powdery mildew originating from *H. bulbosum*, especially line 81882/83/3/2/9 resistant to infection with all isolates used, should be used in breeding programmes to provide farmers with cultivars with highly effective resistance to this disease.

REFERENCES

- Backes G., Madsen L.H., Jaiser H., Stougaard J., Herz M., Mohler V., Jahoor A. 2003. Localisation of genes for resistance against *Blumeria graminis* f.sp. *hordei* and *Puccinia graminis* in a cross between a barley cultivar and a wild barley (*Hordeum vulgare* ssp. *spontaneum*) line. *Theor Appl Genet* 106:353-362.
- Balkema-Boomstra A.G., Mastebroek H.D. 1995. Effect of powdery mildew (*Erysiphe graminis* f. sp. *hordei*) on photosynthesis and grain yield of partially resistant genotypes of spring barley (*Hordeum vulgare* L.). *Plant Breeding* 114:126-130.
- Biffen R.K. 1907. Studies on the inheritance of disease resistance. *J. Agric. Sci., Cambridge* 2:109-128.
- Bonman J.M., Bockelman H.E., Jackson L.F., Steffenson B.J. 2005. Disease and insect resistance in cultivated barley accessions from the USDA National Small Grains Collection. *Crop Sci* 45:1271-1280.
- Bothmer von R., Jacobsen N., Rikke C.B., Jørgensen B., Linde-Laursen I. 1995. An ecogeographical study of the genus *Hordeum*. IPGRI, Rome, Italy, pp 1-129.
- Bothmer von R., Sato K., Knüpfner H., van Hintum T. 2003a. Barley diversity – an introduction, w: Diversity in Barley (*Hordeum vulgare*). Bothmer von R., Hintum van Th., Knüpfner H., Sato K. (red.). Elsevier Science B.V., Amsterdam, The Netherlands: 3 – 8.
- Bothmer von R., Sato K., Komatsuda T., Yasuda S., Fischbeck G. 2003b. The domestication of cultivated barley. In: Bothmer von R, Hintum van Th, Knüpfner H, Sato K (eds), Diversity in Barley (*Hordeum vulgare*). Elsevier Science B.V., Amsterdam, The Netherlands, pp. 9-27.
- Brooks W.S., Griffey C.A., Steffenson B.J., Vivar H.E. 2000. Genes governing resistance to *Puccinia hordei* in thirteen spring barley accessions. *Phytopathol* 90:1131–1136.
- Brown J.K.M., 1996. Fungicide resistance in barley powdery mildew: from genetics to crop protection. In: Kema G.H.J., Niks R.E., Daamen R.A., (eds.), *European and Mediterranean Cereal Rust and Powdery Mildews Conference, Lunteren, The Netherlands*, 259-267.
- Brown J.K.M., Hovmüller M.S. 2002. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Sci* 297:537-541.

- Brian Y.J., Steffenson J., Bockelman H.E. 1995. Evaluation of cultivated and wild barley for resistance to pathotypes of *Puccinia hordei* with wide virulence. *Gen. Res Crop Evol* 42(1):1–6.
- Ceccarelli S., Grando S., van Leur J.A.G. 1995. Barley landraces of the fertile crescent offer new breeding options for stress environments. *Diversity* 11:112-113.
- Czembor H.J. 1976. Sources of resistance of barley to *Erysiphe graminis* f. sp. *hordei*. *Hod Rośl Aklim Nas* 20:467-490.
- Czembor J.H. 1996. Presence and expression of resistance genes to powdery mildew of barley in selections from Tunisian barley landraces. Ph. D. thesis, Department of Plant Pathology, Montana State University, USA, pp 1 – 144.
- Czembor J.H. 2005. Powdery mildew [*Blumeria graminis* (DC.) E. O. Speer f. sp. *hordei*] resistance in landraces of barley (*Hordeum vulgare* L.) – habilitation monography. Monographies and Dissertations of IHAR no. 2005(24), pp 1-164.
- Czembor J.H., Czembor H.J. 1998. Powdery mildew resistance in cultivars of spring barley from Polish Register. *Plant Breed Seed Sci* 42(2):87-99.
- Czembor J.H., Czembor H.J. 1999a. Resistance to powdery mildew in barley landraces collected from Jordan. *Plant Breed Seed Sci* 43(2):65-80.
- Czembor J.H., Czembor H.J. 1999b. Powdery mildew resistance in cultivars of winter barley from Polish Register. *Plant Breed Seed Sci* 43(1):65-75.
- Czembor H.J., Czembor J.H. 2004. Pathogenicity of barley powdery mildew (*Blumeria graminis* f. sp. *hordei*) in Poland in 2000. *Biuletyn IHAR* 233:107-115.
- Czembor J.H. Johnston M.R. 1999. Resistance to powdery mildew in selections from Tunisian barley landraces. *Plant Breed* 118(6):503-509.
- Czembor J.H., Czembor H.J. 2001. Inheritance of resistance to powdery mildew (*Blumeria graminis* f. sp. *hordei*) in selections from Moroccan landraces of barley. *Cereal Res Comm* 29(3-4):281-288.
- Czembor H.J., Czembor J.H. 2007a. Leaf rust resistance in spring barley cultivars and breeding lines. *Plant Breed Seed Sci*, in press.
- Czembor H.J., Czembor J.H. 2007b. Resistance to leaf rust in winter barley cultivars and breeding lines. *Plant Breed Seed Sci*, in press.
- Czembor J.H., Frese L. 2003. Powdery mildew resistance in selections from barley landraces collected from Turkey. *Die Bodenkultur* 54(1):35-40.
- Czembor J.H., Bladenopoulos K. 2007. Resistance to leaf rust (*Puccinia hordei*) in Greek barley cultivars and breeding lines. *Cereal Rusts and Powdery Mildews Bull.*, [www.crpmb.org/] 2007/0215czembor
- Czembor H.J., Gacek E.S., Kudła M.M. 1979. Sources of resistance to barley mildew *Erysiphe graminis* f. sp. *hordei*. *Hod. Rośl. Akł. Nas.* 23(6): 337-355.
- Czembor P.C., Pietrusińska A., Czembor H.J. 2006. Mapping new resistance gene to *Puccinia hordei* Otth. in barley. In: *Cereal Science and Technology for Feeding Ten Billion People: Genomics Era and Beyond*. Proceedings from EUCARPIA – Cereal Section Conference, 13-17 Nov. Lleida, Spain, p 54.
- Eglinton J.K., Evans D.E., Brown A.H.D., Langridge P., McDonald G., Jefferies S.P., Barr A.R. 1999. In: *The use of wild barley (Hordeum vulgare ssp spontaneum) in breeding for quality and adaptation*. Proceedings of 9th Australian Barley Technical Symposium 2.29, pp 1-6.
- Finckh M.R., Gacek E.S., Nadziak J., Wolfe M.S., Czembor H.J. 1996. Ecological interactions in cereal cultivar mixtures in Poland, w: *European and Mediterranean Cereal Rust and Powdery Mildews Conference*. Kema G.H.J., Niks R.E., Daamen R.A. (red.). Lunteren, The Netherlands: 272-274.
- Finckh M.R., Gacek E.S., Czembor H.J., Wolfe M.S. 1999. Host frequency and density effects on powdery mildew and yield in mixtures of barley cultivars. *Plant Pathol.* 48:807-816.
- Finckh M.R., Gacek E.S., Goyeau H., Lannou C., Merz U., Mundt C.C., Munk L., Nadziak J., Newton A.C., de Vallaville-Pope C., Wolfe M.S. 2000. Cereal variety and species mixtures in practice, with emphasis on disease resistance. *Agronomie* 20:813-837.
- Fischbeck G 2003. Diversification through breeding. In: *Bothmer von R, Hintum van Th, Knüpffer H, Sato K (Eds), Diversity in Barley (Hordeum vulgare)*, Elsevier Science B.V., Amsterdam, The Netherlands, pp. 29-52.
- Fetch T.Jr., Pickering R.A., Johnston P.A. 2004. Novel stem rust resistance in barley lines with introgressions of *Hordeum bulbosum* chromatin. 11th International Cereal Rusts and Powdery Mildews Conference: Abstracts, Norwich, England, 24-27 August 2004:A2.18.
- Flor H.H. 1956. The complementary genetic systems in flax and flax rust. *Adv Genet* 8:29-54.
- Griffiths E. 1984. Foliar diseases: the damage caused and its effect on yield. In: Wood, I.K.S., G.J. Jellis (eds.), *Plant Diseases: infection, damage and loss*, Blackwell Scientific Publications, Oxford, 149-159,
- Gullino M.L., Kuijpers L.A.M. 1994. Social and political implications of managing plant diseases with restricted fungicides in Europe. *Ann Rev Phytopathol* 32:559-79.
- Honecker L. 1938. Über die physiologische Spezialisierung des Gerstenmeltaues als Grundlage für die Immunitätszüchtung. *Züchter* 10:169-181.
- Jin Y., Steffenson B.J., Bockelman H.E. 1995. Evaluation of cultivated and wild barley for resistance to pathotypes of *Puccinia hordei* with wide virulence. *Gen Res Crop Evol* 42:1-6.
- Jönsson R., Lehmann L. 1999. Use of new gene sources for resistance in barleybreeding. *Sver Utsadesfor Tidsskr* 109(3):146-159.

- Jørgensen J.H. 1994. Genetics of powdery mildew resistance in barley. *Crit. Rev. Plant Sci.* 13(1):97-119.
- Jørgensen J.H., Jensen H.P. 1997. Powdery mildew resistance in barley landrace material. I. Screening for resistance. *Euphytica* 97:227-233.
- Kasha K.J., Kao K.N. 1970. High frequency haploid production in barley (*Hordeum vulgare* L.). *Nature* 225:874-876.
- Kølster P., Munk L., Stølen O., Lihde J. 1986. Near-isogenic barley lines with genes for resistance to powdery mildew. *Crop Sci* 26:903-907.
- Lehmann L. 1991. The use of genetic resources for isolating disease resistance for barley cultivar development. In: Munck L (Ed), *Proceedings 6th Barley Genetics Symposium Volume I*, pp. 650-652.
- Lehmann L., von Bothmer R. 1988. *Hordeum spontaneum* and land races as a gene resource for barley breeding. In M.L. Jorna and L.A.J. Sloodmaker (eds) *Cereal Breeding Related to Integrated Cereal Production*. Pudoc, Wageningen, The Netherlands. pp. 190-194.
- Lehmann L.C., Jönsson R., Gustafsson M. 1998. Identification of resistance genes to powdery mildew isolated from *Hordeum vulgare* ssp. *spontaneum* and land races of barley. *Sverig Utsadesfor Tidskr* 108(2): 94-101.
- Leijerstam B. 1996. Sources of resistance to powdery mildew, *Erysiphe graminis* f.sp. *hordei*, in barley. *Sverig Utsadesfor Tidskr* 106(2) 64-68.
- Leur van J.A.G., Ceccarrelli S., Grando S. 1989. Diversity for disease resistance in barley landraces from Syria and Jordan. *Plant Breed* 103: 324-335.
- Levine M.N., Cherewick W.J. 1952. Studies on dwarf leaf rust of barley. U.S. Department of Agric. Tech. Bull. No. 1056, Washington, DC, pp 1-17.
- Limpert E., Godet F., Muller K. 1999. Dispersal of cereal mildews across Europe. *Agric. For. Meteorol.* 97:293-308.
- Limpert E., Bartos P., Graber W.K., Muller K., Fuchs J.G. 2000. Increase of virulence complexity of nomadic airborne pathogens from west to east across Europe. *Acta Phytopathologica et Entomologica Hungarica* 35:261-272.
- Lim L.G., Gaunt R.E. 1986. The effect of powdery mildew (*Erysiphe graminis* f. sp. *hordei*) and leaf rust (*Puccinia hordei*) on spring barley in New Zealand. I. Epidemic development, green leaf area and yield. *Plant Pathol* 35:44-53.
- Lundqvist A. 1962. Self-incompatibility in diploid *Hordeum bulbosum* L. *Hereditas* 48:38-152.
- Mains E.B., Dietz S.M. 1930. Physiologic forms of barley mildew, *Erysiphe graminis hordei* Marchal. *Phytopathol* 20:229-239.
- Martinez F., Niks R.E., Rubiales D. 2001. Partial resistance to leaf rust in a collection of ancient Spanish barleys. *Hereditas* 135:199-203.
- Michel M., Proeseler G., Scholz M., Pickering R., Melz G. 1994. Transfer von *H. bulbosum* - Genen in die Kulturgerste. *Vortr. Pflanzenzüchtung* 28:87-189.
- McDonald B.A., Linde C. 2002. The population genetics of plant pathogens and breeding strategies for durable resistance. *Euphytica* 124:163-180.
- Munk L., Jensen H.P., Jørgensen J.H., 1991. Virulence and disease severity of barley powdery mildew in Denmark 1974-1989. In: Jørgensen J.H. (ed.), *Integrated Control of Cereal Mildews: Virulence Patterns and Their Change*, Risø National Laboratory, Roskilde, Denmark, 55-65.
- Müller K., McDermott J.M., Martin M.S., Limpert E., 1996. Analysis of diversity of plant pathogens: the barley powdery mildew pathogen across Europe. *Europ. J Plant Pathol.* 102: 385-395.
- Negassa, M. 1985. Geographic distribution and genotypic diversity of resistance to powdery mildew of barley in Ethiopia. *Hereditas* 102: 113- 121.
- Nevo E. 1985. Origin, evolution, population genetics and resources for breeding of wild barley, *Hordeum spontaneum*, in the fertile crescent. In: Shewry PR (Ed), *Barley: Genetics, Biochemistry, Molecular Biology and Biotechnology*, CAB International, Wallingford, pp. 19-43.
- Nierobca A., Horoszkiewicz-Janka J., Czembor J.H. 2003. Plant protection as an important element of cereals cultivation technology in the European Union. *Pamiętnik Pulawski* 132:311-320.
- Nover I., Lehman C.O. 1973. Resistenzeigenschaften im gersten- und weizensortiment Gatersleben 17. Prüfung von sommergersten auf ihr verhalten gegen mehltau (*Erysiphe graminis* DC. f. sp. *hordei* Marchal). *Kulturpflanze* 21: 275-294.
- Ochoa J., Parlevliet J.E. 2007. Effect of partial resistance to barley leaf rust, *Puccinia hordei*, on the yield of three barley cultivars. *Euphytica* 153(3):309-312.
- Parlevliet J.E. 1976. The genetics of seedling resistance to leaf rust, *Puccinia hordei* Otth, in some spring barley cultivars. *Euphytica* 25:249-254.
- Parlevliet J.E. 1983. Race-specific resistance and cultivar-specific virulence in barley-leaf rust pathosystem and their consequences for breeding of leaf rust resistant barley. *Euphytica* 32:367-375.
- Parlevliet J.E., van Ommeren A. 1975. Partial resistance of barley to leaf rust, *Puccinia hordei*. II. Relationship between field trials, micro plot test and latent period. *Euphytica* 35:267-272.
- Pickering R.A. 1980. Attempts to overcome partial incompatibility between *Hordeum vulgare* L. and *H. bulbosum* L. *Euphytica* 29:369-377.

- Pickering R.A. 1981. Pollen tube-stylodium interaction in *Hordeum vulgare* L. × *H. bulbosum* L. 1981. Pp. 666-676. In: M.J.C. Asher, R.P. Ellis, A.M. Hayter, R.N.H. Whitehouse (Eds), Proceedings of the 4th International Barley Genetics Symposium.
- Pickering R.A. 1983. The location of a gene for incompatibility between *Hordeum vulgare* L. and *H. bulbosum* L. *Heredity* 51:455-459.
- Pickering R.A. 1984. The influence of genotype and environment on chromosome elimination in crosses between *Hordeum vulgare* L. × *H. bulbosum* L. *Plant Sci Letters* 34:153-164.
- Pickering R.A. 1987. The influence of *Hordeum bulbosum* L. ploidy level on crossability with *H. vulgare* L. cv. Vada and *Triticum aestivum* L. cv. Chinese spring. *Barley Genet Newsl* 17: 43-45.
- Pickering R.A. 1988. The production of fertile triploid hybrids between *Hordeum vulgare* L. (2n = 2x = 14) and *H. bulbosum* L. (2n = 4x = 28). *Barley Genet Newsl* 18:25-29.
- Pickering R.A. 1994. The chromosome stability of *Hordeum vulgare* L. - *Hordeum bulbosum* L. chromosome substitution plants grown at two temperatures. *Hereditas* 121(1):39-43.
- Pickering R.A. 2000. Do the wild relatives of cultivated barley have a place in barley improvement?. *Barley Genetics VIII. Proceedings of the 8th International Barley Genetics Symposium, Adelaide, Australia, 22-27 October, 2000* 1:223-230.
- Pickering R.A., Devaux P. 1992. Haploid production: approaches and use in plant breeding. In: Shewry PR (Ed), *Barley: Genetics, Biochemistry, Molecular Biology and Biotechnology*, CAB International, Wallingford, pp. 519-547.
- Pickering R.A., Hayes J.D. 1976. Partial incompatibility in crosses between *Hordeum vulgare* L. and *H. bulbosum* L. *Euphytica* 25:671-678.
- Pickering R.A., Johnston P.A. 2005. Recent progress in barley improvement using wild species of *Hordeum*. *Cytogenet Genome Res* 109:344-349.
- Pickering R.A., Rennie W.F. 1990. The evolution of superior *Hordeum bulbosum* L. genotypes for the use in a doubled haploid barley breeding program. *Euphytica*: 45:251-255.
- Pickering R.A., Rennie W.F., Cromey M.G. 1987. Disease resistant material available from the wide hybridization programme at DSIR. *Barley Newsletter* 31:248-250.
- Pickering R.A., Timmerman G.M., Cromey M.G., Melz G. 1994. Characterisation of progeny from backcrosses of triploid hybrids between *Hordeum vulgare* L. (2x) and *H. bulbosum* L. (4x) to *H. vulgare*. *Theor Appl Genet* 88:460-464.
- Pickering R.A., Hill A.M., Michel M., Timmerman-Vaughan G.M. 1995. The transfer of a powdery mildew resistance gene from *Hordeum bulbosum* L. to barley (*H. vulgare* L.) chromosome 2 (21). *Theor Appl Genet* 91:1288-1292.
- Pickering R.A., Steffenson B.J., Hill A.M., Borovkova I. 1998. Association of leaf rust and powdery mildew resistance in a recombinant derived from a *Hordeum vulgare* × *H. bulbosum* hybrid. *Plant Breed* 117:83-84.
- Pickering R.A., Johnston P.A., Forbes E.M., Timmerman-Vaughan G.M., Cromey M.G., Steffenson B.J., Schubert I., Proesler G., Zhang L., Murray B.J. 1999. *Hordeum bulbosum* is an exploitable source of disease resistance genes for barley breeders. In: Proceedings of 9th Australian Barley Technical Symposium, Melbourne, Australia, 12-16 Sept, 1999: 2.28, pp 1-4.
- Pickering R.A., Malyshev S., Künzel G., Johnston P.A., Korzun V., Menke M., Schubert I. 2000a. Locating introgressions of *Hordeum bulbosum* chromatin within the *H. vulgare* genome. *Theor Appl Genet* 100:27-31.
- Pickering R., Johnston P.A., Timmerman - Vaughan G.M., Cromey M.G., Forbes E.M., Steffenson B.J., Fetch Jr.T.G., Zhang L., Murray B.G., Proesler G., Habekuß A., Kopahnke D., Schubert I. 2000b. *Hordeum bulbosum* – A new source of disease and pest resistance genes for use in barley breeding programmes. 30:6-9.
- Pickering R., Niks R., Johnston P.A., Butler R. 2004a. Importance of the secondary gene pool in barley genetics and breeding. II. Disease Resistance, agronomic performance and Quality. *Czech J Genet Plant Breed* 40:79 -85.
- Pickering R.A., Hudakova S., Houben A., Johnston P.A., Butler R.C. 2004b. Reduced metaphase I associations between the short arms of homologous chromosomes in a *Hordeum vulgare* L. × *H. bulbosum* diploid hybrid influences the frequency of recombinant progeny. *Theor Appl Genet* 109:911-916.
- Pickering R., Klatt S., Butler R.C. 2005. Reduced chromosome association between the short arms of 5H homologues in *Hordeum vulgare* L. at metaphase I. *Plant Breed* 124:416-418.
- Pickering R., Klatt S., Butler R.C. 2006a. Identification of all chromosome arms and their involvement in meiotic homoeologous associations at metaphase I in 2 *Hordeum vulgare* L. × *Hordeum bulbosum* L. hybrids. *Genome* 2006, 49:73-78.
- Pickering R., Ruge-Wehling B., Johnson P.A., Schweizer G., Ackermann P., Wehling P. 2006b. The transfer of a gene conferring resistance to scald (*Rhynchosporium secalis*) from *Hordeum bulbosum* into *H. vulgare* chromosome 4HS. 125:576-579.
- Pohler W., Szigat G. 1982. Versuche zur rekombinanten Genübertragung von der Wildgerste *Hordeum bulbosum* auf die Kulturgerste *H. vulgare*. 1. Mitt. Die Rückkreuzung VV × BBVV. *Arch Züchtungsforsch.*, Berlin 12:87-100, 1982).
- Ralski E., Mikołajewicz T. 1958. Studies on susceptibility of barley varieties to powdery mildew (*Erysiphe graminis* ED.C. f.sp. *hordei* Marchal). *Hodowla Roślin* 2: 313-332.

- Ruge B., Linz A., Pickering R., Proeseler G., Greif P., Wehling P. 2003. Mapping of *Rym14^{Hb}*, a gene introgressed from *Hordeum bulbosum* and conferring resistance to BaMMV and BaYMV in barley. *Theor Appl Genet* 107:965–971.
- Ruge B., Linz A., Ackermann P., Habekuss A., Schweizer G., Pickering R.A., Wehling P. 2005. Kartierung von resistenz bedingenden Hordeum-bulbosum-Introgressionen im gerstengenom. *Vortrage für Pflanzenzüchtung* 67:166-177.
- Russell J.R., Ellis R.P., Thomas W.T.B., Waugh R., Provan J., Booth A., Fuller J., Lawrence P., Young G., Powell W. 2000. A retrospective analysis of spring barley germplasm development from 'foundation genotypes' to currently successful cultivars. *Mol Breed* 6:553–568.
- Shtaya M.J.Y., Sillero J.C., Rubiales D. 2006a. Search of partial resistance against *Puccinia hordei* in barley landraces from the Fertile Crescent. *Plant Breed* 125:343-346.
- Shtaya M.J.Y., Sillero J.C., Rubiales D. 2006b. Screening for resistance to leaf rust (*Puccinia hordei*) in collections of Spanish barleys. *Breed Sci* 56:173-177.
- Shtaya M.J.Y., Sillero J.C., Rubiales D. 2006c. Search for resistance against *Blumeria graminis* in barley landraces from Fertile Crescent. *Barley Newsletter* 49 <http://wheat.pw.usda.gov/ggpages/BarleyNewsletter/49/SpainBNL49.htm>
- Shtaya M.J.Y., Sillero J.C., Flath K., Pickering R., Rubiales D. 2007. The resistance to leaf rust and powdery mildew of recombinant lines of barley (*Hordeum vulgare* L.) derived from *H. vulgare* x *H. bulbosum* crosses. *Plant Breed* 126:259-267.
- Smit G., Parlevliet J.E. 1990. Mature plant resistance of barley to leaf rust, another type of resistance. *Euphytica* 50:159-162.
- Steffenson B.J. 1998. Coordinator's report: Disease and pest resistance genes. *Barley Gen Newsl* 28:95-98.
- Steffenson B.J. 1999. Coordinator's report: Disease and pest resistance genes. *Barley Gen Newsl* 29:62-66.
- Szigat G., Szigat G. 1991. Amphidiploid hybrids between *Hordeum vulgare* and *H. bulbosum* – basis for the development of new initial material for winter barley breeding. *Vortr Pflanzenzüchtg* 20:34–39.
- Thomas H.M., Pickering R.A. 1985. The influence of parental genotype on the chromosome behaviour of *Hordeum vulgare* x *H. bulbosum* diploid hybrids. *Theor Appl Genet* 71:437–442.
- Thomas W.T.B 2003. Prospects for molecular breeding of barley. *Ann Appl Biol* 142:1–12.
- Thörn E.C. 1992a. The influence of genotype and environment on seed and embryo development in barley (*Hordeum vulgare* L.) after crossing with *Hordeum bulbosum* L. *Euphytica* 59:109-118.
- Thörn E.C. 1992b. Embryo development in two barley genotypes after self pollination and pollination with *Hordeum bulbosum* L. *Euphytica* 65:93-98.
- Walther U., Rapke H., Proeseler G., Szigat G. 2000. *Hordeum bulbosum* – a new source of disease resistance – transfer of resistance to leaf rust and mosaic viruses from *H. bulbosum* into winter barley. *Plant Breed* 119:215–218.
- Weibull J., Walther U., Sato K., Habekuß A., Kopahnke D., Proeseler G. 2003. Diversity in resistance to biotic stresses. In: von Bothmer R, Van Hintum Th, Knüpfper H, Sato K (Eds), *Diversity in Barley (Hordeum vulgare)*, Elsevier Science B.V., Amsterdam, The Netherlands, pp. 143-178.
- Wiberg A. 1974. Sources of resistance to powdery mildew in barley. *Hereditas* 78: 1-40.
- Wolfe M.S. 1984. Trying to understand and control powdery mildew. *Plant Pathol* 33: 451-466.
- Wolfe M.S. 1993. Can the strategic use of disease resistant hosts protect their inherent durability?, w: *Durability of Disease Resistance*. Jacobs Th., Parlevliet J.E. (red.). Kluwer Academic Publishers, The Netherlands: 83-96.
- Wolfe M.S., McDermott J.M. 1994. Population genetics of plant pathogen interactions: the example of the *Erysiphe graminis-Hordeum vulgare* pathosystem. *Ann Rev Phytopath* 32: 89-113.
- Wolfe M. S., Schwarzbach E. 1978. The recent history of the evolution of barley powdery mildew in Europe. In: Spencer D. M. (ed.) *The Powdery Mildews*, pp. 129-157. Academic Press, London.
- Xu J., Kasha K.J. 1992. Transfer of a dominant gene for powdery mildew resistance and DNA from *Hordeum bulbosum* into cultivated barley (*Hordeum vulgare*). *Theor Appl Genet* 84:771–777.
- Xu J., Snape J.W. 1988. The cytology of hybrids between *Hordeum vulgare* and *H. bulbosum* revisited. *Genome* 30:486–494.
- Xu J., Snape J.W. 1989. The resistance of *Hordeum bulbosum* and its hybrids with *H. vulgare* to common fungal pathogens. *Euphytica* 41:273-276.
- Zeller F.J. 1998. Nutzung des genetischen Potentials der *Hordeum*-Wildarten zur Verbesserung der Kulturgerste (*Hordeum vulgare* L.). *Angewandte Botanik* 72:162-167.
- Zine Elabbidine F., Reinhold M., Scharen A.L. 1992. Effect of barley powdery mildew infection on barley under simulated drought stress. *Cereal Rusts & Powdery Mildews Biull* 20: 1-6.
- Zhang L., Pickering R., Murray B. 1999. Direct measurement of recombination in interspecific hybrids between *Hordeum vulgare* and *H. bulbosum* using genomic in situ hybridization. *Heredity* 83:304–309.
- Zhang L., Pickering R.A., Murray B.G. 2001. A *Hordeum vulgare* x *H. bulbosum* tetraploid hybrid provides useful agronomic introgression lines for breeders. *NZ J Crop and Hort Sci* 29:239–246.
- Zhang L., Murray B.G., Pickering R.A. 2002. Variable patterns of chromosome synapsis at pachytene in *Hordeum vulgare* x *H. bulbosum* hybrids and their parents. *Hereditas* 137:90–95.