Euphytica (2007) 153:295–308
DOI 10.1007/s10681-006-9236-y

Quantitative resistance and its components in 16 barley cultivars to yellow rust, *Puccinia striiformis* f. sp. *hordei*

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Received: 21 April 2005 / Accepted: 11 July 2006 / Published online: 30 August 2006

Abstract Sixteen barley cultivars with a susceptible infection type (IT = 7–8) in the seedling stage to an isolate of race 24 of *Puccinia striiformis* f. sp. *hordei* were planted at two locations in México. Disease severity (DS) parameters were assessed for the flag leaf and for the upper three leaves. The cultivars represented at least five levels of quantitative resistance ranging from very susceptible to quite resistant. ''Granado'', ''Gloria/Copal'' and ''Calicuchima-92'' represented the most resistant group and had an IT of 7 or 8. The cultivar × environment interaction variance, although significant, was very small compared with the cultivar variance. The disease severity parameters were highly correlated. The monocyclic parameter DS_m, measured when the most susceptible cultivar had reached its maximum DS, was very highly correlated with the area under the disease progress curve (AUDPC), r being 0.98.

Components of quantitative resistance were evaluated in two plant stages. In the seedling stage small cultivar effects for the latency period were observed, which were not correlated with the quantitative resistance measured in the field. In the adult plant stage the latency period (LP), infection frequency (IF) and colonization rate (CR) were measured in the upper two leaves. The LP was much longer than in the seedling stage and differed strongly between cultivars. The differences in IF were too large, those in CR varied much less. The components showed association with one another. The LP and IF were well correlated with the AUDPC (r = 0.7–0.8).

Keywords Barley · Disease severity · Durable resistance · Colonization rate · Infection frequency · Latency period · *Puccinia striiformis* f. sp. hordei · Quantitative resistance · Resistance components · Yellow rust

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Introduction

Yellow rust (*P. striiformis* f. sp. *hordei*) in barley (*Hordeum vulgare*) occurs worldwide and is a major disease in various parts of South, Central and North America (Dubin and Stubbs 1986; Chen et al. 1994; Roelfs and Huerta-Espino 1994; Sandoval-Islas et al. 1998). There are different strategies for controlling the disease, but genetic resistance is the more economically and environmentally appropriate option (Broers and Jacobs 1989). The economic value of genetic resistance depends on both its level and durability (Denissen 1993).

As in other cereal–rust pathosystems, in the barley–yellow rust pathosystem two types of resistance can be discerned, the hypersensitivity reaction and the quantitative resistance (Osman-Ghani and Manners 1985; Sandoval-Islas et al. 1998). The former type is usually inherited in a major genic way, is typically race-specific and non-durable. The latter tends to be of a polygenic or oligogenic nature and is often highly durable (Parlevliet 1993). The durability of quantitative resistance has been demonstrated in various other cereal–rust pathosystems (Parlevliet 1979; Van Ginkel and Rajaram 1993; Broers et al. 1996). Also some barley cultivars with high levels of quantitative resistance, such as ''UNA-80'', ''IBTA-80'', ''Kolla'', ''Terán-78'' and ''Calicuchima-92'', that were released in South America by national programs in the late 1970s and early 1980s, are still resistant to yellow rust.

Many barley cultivars with hypersensitive resistance to yellow rust have been released (Bakshi and Luthra 1971; Roane 1972; Parlevliet 1976; Stubbs 1985), but with this kind of resistance, the fungal population is able to adapt genetically, resulting in a loss of effectiveness of the resistance (Broers and Jacobs 1989).

In both spring and winter barley it has been found that some cultivars have high infection types in the seedling stage associated with high levels of quantitative resistance in the adult plant stage (Osman-Ghani and Manners 1985; Sandoval-Islas et al. 1998).

Although quantitative resistance has been studied in detail in other cereal–rust pathosystems, little information is available for the barley–yellow rust pathosystem. Quantitative resistance to *P. hordei* in barley (Parlevliet and Van Ommeren 1975) and to *P. triticina* in wheat is partial (Ohm and Shaner 1976; Broers 1989b), and is characterized by a susceptible infection type (IT) in both the seedling and the adult plant stages combined with a slow rate of disease development. It is therefore partial sensu Parlevliet (Parlevliet and Van Ommeren 1975). By contrast, quantitative resistance to wheat yellow rust is not partial sensu Parlevliet since it is characterized by a susceptible infection type in the seedling stage and reduced rate of disease development, but the infection type in the adult plant stage is not necessarily a susceptible one (Broers 1993, 1997; Broers et al. 1996; Park and Rees 1989).

Wheat and barley cultivars with quantitative resistance to yellow and leaf rust tend to have a long latency period, a low infection frequency, a decreased spore production and a short infectious period (Parlevliet 1975; Denissen 1993; Broers and Jacobs 1989; Broers 1997). Latency period is the most important component of quantitative resistance in these pathosystems (Parlevliet and Van Ommeren 1975; Neervoort and Parlevliet 1978; Broers and Jacobs 1989). The degree of association between these resistance components depends on the pathosystem (Parlevliet 1975; Broers 1989a, 1997; Wilson and Shaner 1989; Habtu and Zadoks 1995).

In several cereal–rust pathosystems the quantitative aspects of cultivar resistance have been described by means of the disease severity (DS) at a certain moment or plant development stage, the area under the disease progress curve (AUDPC) or by means of the apparent infection rate, *r*, (Parlevliet 1979; Steffenson and Webster 1992; Broers et al. 1996; Shaner 1996).

This paper studies the quantitative resistance and its components to yellow rust in a range of barley cultivars in three different environments to obtain some insight into the range of quantitative resistance already available in elite material and the stability of the expression of this character.

Materials and methods

Field experiments

Toluca valley

Fifteen barley cultivars from the breeding programs of ICARDA–CIMMYT and INIFAP (Mexico) with different levels of quantitative resistance to yellow rust, *P. striiformis* f. sp. *hordei*, were sown in the summer season in the experimental fields of CIMMYT in Atizapan near Toluca, Mexico. To create different environments two sowing dates were used, 23 May and 8 June.

Both experiments were sown adjacent to each other in a complete block design with three replicates at a rate of 80 kg/ha. A plot consisted of two beds each of two rows of 2.0 m length. The beds were 0.75 m apart, the rows within beds 0.20 m. The distance between plots was 0.75 m. The blocks were separated from each other by a path perpendicular to the direction of the plot rows into which a spreader row of the susceptible cultivar Cerro Prieto was sown. The yellow rust epidemic was initiated by inoculating a number of plants in the spreader rows when the plants were in the development stage 20–30 on the scale of Zadoks et al. (1974), about 5½ weeks after sowing. The plants were inoculated by injecting them with 0.5 ml of a spore suspension of *P. striiformis* f. sp. *hordei*, isolate Mex-1, of race 24 (Sandoval-Islas et al. 1998). The suspension was obtained by suspending 2 g of spores per litre of water onto which five drops of Tween 20 were added.

Celaya

The experiment was sown at the Agricultural Experiment Station of INIFAP near Celaya at 25 November with the same cultivars, except ''Arupo'', which was substituted by ''Apizaco''. The experiment consisted of a complete block design with four replicates. Each plot had six rows of 4.0 m length and 0.30 m apart. The plots were separated by 0.60 m. The seed rate was 80 kg/ha. As in Toluca, a spreader row with a susceptible cultivar was planted in the paths separating the blocks. The inoculation, about 3½ weeks after sowing, was as in Toluca.

Field assessments

The assessment of the DS started when all cultivars had developed the flag leaf, development stage 39–41 on the scale of Zadoks et al. (1974). Seven assessments (six for Toluca sowing 1), each a week apart, were taken to be used to calculate the AUDPC. At each assessment date 12 tillers per plot were taken at random from the two central rows and stored in plastic bags in a refrigerated room kept at below 10°C. In the next 2 days all samples were assessed. Of each of 10 tillers per sample the DS expressed as the percentage leaf area affected using the modified Cobb scale (Peterson et al. 1948), the development stage according to Zadoks et al. (1974) and the infection type (IT) according to McNeal et al. (1971) were assessed.

The DS was assessed on the flag leaves and on the upper three leaves. It was measured when the highly susceptible control cultivar reached its maximum disease level, DS_m (flag leaf) and DS_m (upper three leaves), and when the cultivars, which differed in earliness, reached development stage 60, DS_{60} (flag leaf) and DS_{60} (upper three leaves).

Greenhouse and growth room experiments

The experiments were carried out at CIMMYT, El Batán, Mexico with the same 16 cultivars as used in the field experiments. All cultivars had a susceptible infection type in the seedling stage and varied for their DS in the field. Seedlings and adult plants were inoculated with the same isolate as used in the field experiments.

Seedling experiments

Per cultivar 20 seeds were sown in rows in plastic trays ($40 \times 30 \times 10$ cm) with a mixture of soil, peat moss and sand in a 7:5:5 proportion. Each of the two experiments consisted of a randomized complete block design with four replications, each block consisting of two trays. Eight cultivars were randomized within each tray. Eight days old seedlings, stage 10, were inoculated with a uredospore–Soltrol suspension (8×10^5 uredospores/ml). Seedlings were incubated for 16 h in a moist chamber at 100% relative humidity, in the

dark at 15°C. After incubation, the seedlings were transferred to a greenhouse with temperature ranges of 15–20/15–18°C night/day and 14 h of light. After the first flecks were observed, seedlings were examined every day to detect the presence of sporulation. The seedling latency period 1 (SLP_1) was defined as the number of days between the start of incubation and the first sporulating infection detected in one of the seedlings of a cultivar. The SLP_{50} was estimated as the time at which 50% of the seedlings of each cultivar were sporulating and was calculated by linear interpolation as described by Parlevliet (1975) for barley leaf rust. The DS of each seedling (SDS) was assessed using a modified Cobb scale, which is a pictorial scale (Peterson et al. 1948). The IT was rated according to the scale (0 = immune to 9 = fully susceptible) of McNeal et al. (1971).

Adult plant experiments

Per cultivar seven seeds were sown in plastic pots (18 cm in diameter) in a greenhouse. Ten days later five seedlings per pot were kept. The plants were fertilized every 14 days with 4 g of a mixture of triple calcium superphosphate and urea in a 1:2 proportion. Sowing was performed at weekly intervals over a period of 6 weeks to ensure the availability of sufficient plants of each cultivar at the same development stage, 47–49. Inoculations were carried out at this stage, when flag leaves were young and fully developed.

Four experiments were carried out each using a randomized complete block design with four replications. Each replication consisted of 16 pots, each pot with five plants of a cultivar and only one tiller per plant was inoculated. In experiments one to three, the flag leaf (FL) and the leaf below the flag leaf (FL-1) of each randomly selected tiller were inoculated with fresh uredospores. The inoculation technique, using inoculated water agar pieces followed the procedures described by Broers and López-Atilano (1994). One water agar piece (1.0 × 2.0 cm) with ca. 1,500 spores/cm^2 was put in the central part of the adaxial side of each FL and FL-1. Incubation was done as with the seedlings. Subsequently the plants were transferred to a greenhouse with day/night temperatures of 18/16°C and 14 h of light. The fourth experiment was carried out with a different inoculation technique. The FL and FL-1 were inoculated with a mixture of 14 mg of fresh uredospores and 36 mg of spores of *Lycopodium*, using a paintbrush (size 5). After inoculation, plants were treated as in experiments 1–3.

The latency period 1 (LP_1) was defined as the number of days between the start of incubation and the first sporulating uredosorus on any one inoculated leaf of a cultivar. The latency period 50 (LP_{50}) and the infection frequency (IF) were both measured in the following way. A leaf was divided into several longitudinal areas using largeleaf veins as separators (Broers and López-Atilano 1994). After the LP_1 was registered, the number of sporulating stripes in these areas was counted daily until the number did not vary for 3 days. The LP_{50} was assessed when 50% of sporulating stripes were present and was calculated by linear interpolation as described by Parlevliet (1975). The IF was equal to the total number of sporulating stripes divided by the width of the leaf in cm where the water agar piece was placed. The lesion length was measured twice at 10 and 20 days after the LP_{50} was reached. Therefore, measurements were taken at different times for each cultivar. In this way a large part of the variation due to genotypic differences in latency period was removed. To calculate the colonization rate (CR), the difference in lesion length at the first and second measurement was divided by 10. In order to calculate the error variance of the infection frequency (IF), the spore concentration in each experiment was estimated by counting the spores on greased slides placed in the settling tower next to the water agar pieces. The IT was assessed only in experiment 4, 30 days after inoculation.

Statistical analysis

Field experiments

The AUDPC was calculated using the formula of Campbell and Madden (1990) for the flag leaf alone and for the three upper leaves together. The

Weibull probability density function and cumulative distribution can be successfully used to describe a wide range of disease progress curves (Pennypacker et al. 1980; Mora-Aguilera et al. 1996). In this formula b is a scale parameter, which is inversely related to the rate of disease increase. The value b^{-1} is similar, but not the same as the apparent infection rate r of Vanderplank (1963).

The differences between cultivar means of the various parameters over the three experiments (environments) were tested with the Duncan's New Multiple Range test using the combined Genotype × Environment and Error variance as calculated from the analysis of variance. Per experiment a covariance analysis was carried out between the DS_m (flag leaf) and DS_m (upper three leaves) and the development stage because of the cultivar differences in earliness. Both the Pearson linear correlation coefficients and the Spearman rank correlation coefficients were calculated because of non-normality of the distributions.

Greenhouse and growth room experiments

All experiments were analysed using a randomized complete block design with four replications. The least significant difference values (LSD at $P \leq 0.05$) are given except for those of the infection frequencies as these deviated too strongly from a normal distribution. An analysis of variance (ANOVA) was carried out for SLP_{50} and SDS. For adult plant experiments, the experimental unit was the pot mean obtained by averaging the data of the five tillers per pot. ANOVA calculations were performed on the basis of resistance components, leaves and experiments. Pearson linear correlation coefficients were calculated between components across cultivars except for those where the infection frequencies were involved. In those cases the Spearman rank correlation was calculated. The role of the adult plant resistance components on the observed variation in the DS_m, the AUDPC and the b^{-1}, was tested through multiple regression analyses.

All statistical analyses were performed with the SAS software package, version 6.09 (SAS Institute Inc. 1988).

Results

Field experiments

The DS data of the flag leaf and those of the upper three leaves followed the same pattern and were highly correlated in all three experiments. The mean (over three experiments) Pearson linear correlation coefficients for the DS_m and the DS_{60} between those of the flag leaves and those of the upper three leaves were 0.98 and 0.97, respectively. Therefore only the data for the upper three leaves are presented here.

The covariance analysis between the DS_m and the development stage (earliness) showed that the cultivar differences in earliness had no significant effect on the DS_m in any of the experiments. The variance analysis over the three experiments, carried out on the 14 cultivars tested in all experiments (Table 1) showed highly significant effects for environments (experiments), cultivars and cultivar × environment interactions for each of the four DS parameters. The cultivar × environment

Table 1 Analysis of variance of the disease severity when the most susceptible cultivar reached its maximum (DS_m), when the cultivars reached development stage 60 (DS_{60}), of the area under the disease progress curve (AUDPC) and of the disease increase rate (b^{-1}) of 14 barley cultivars (CV) in three environments (E) when exposed to yellow rust, *Puccinia striiformis* f. sp. *hordei*

Source of variation	n	DS_m		DS_{60}		AUDPC		b^{-1}	
		MS	F*	MS	F*	MS	F*	MS	F*
E	2	171	10	582	21	396,397	47	0.001700	134
Repl. within E	7	51	3	76	3^{S}	70,806	8	0.000018	1^{NS}
CV	13	9,815	593	4,361	158	490,0579	583	0.002400	186
CV × E	26	259	16	159	6	162,377	19	0.000320	25
Error	91	16.5		27.7		8,404		0.000013	

*All F-values highly significant ($P \leq 0.01$), except two, which were significant at $P \leq 0.05$ (^{S}) or not significant (^{NS})

interaction effects, however, were very small compared with the cultivar effects.

The first infections in the plots in the three experiments appeared when all cultivars had developed their flag leaves. After that the epidemics developed very well. There were considerable differences in the rate of disease increase between cultivars resulting in large differences in the DS measured as DS_m, DS_{60} or AUDPC (Tables 2, 3). The cultivar Apizaco appeared very susceptibe, followed by a group of quite susceptible cultivars like Trompillo, Guanajuato, Cerro Prieto, Arupo and Puebla. ''Esperanza'' and ''Esmeralda'' can be considered moderately susceptible, while cultivars such as Calicuchima-92, Gloria/Copal and Aleli appeared quite resistant. Of the 16 cultivars 13 had a basically susceptible IT (7 or 8) and only three, ''Esmeralda'', ''Maris/Mink'' and ''Aleli'' had a lower IT (Table 3).

The four parameters are strongly correlated with each other (Table 4). The DS_{60} is the parameter which is the least correlated with the other three. The DS_m and the AUDPC are very highly correlated with a correlation coefficient of at least 0.98.

Although the cultivar × environment interaction variance was significant it was very small compared with the cultivar variance (Table 1). This is born out by the high correlation coefficients between the three environments for all four epidemiological parameters of the cultivars. The Pearson and Spearman correlation coefficients between the two sowings in Toluca were on average 0.97 and 0.93, respectively, while the corresponding r values between the Toluca sowings and the Celaya sowing were 0.91 and 0.87. This indicates that the greater part of the cultivar × environment interaction variance came from the sowing in Celaya (Table 5). A considerable part of this small G × E interaction variance comes from ''Centinella''. This cultivar seemed more susceptible in Toluca than in Celaya.

Greenhouse and growth room experiments

Seedling experiments

Seedling latency period 1 (SLP_1) did not vary among cultivars. SLP_{50}, on the other hand,

Table 2 Mean disease severity (DS) when the most susceptible cultivar reached its maximum DS (DS_m), mean DS when the cultivars were at plant stage 60 (DS_{60}), mean area under the disease progress curve (AUDPC) and mean disease increase rate (b^{-1}) × 100 in three experiments of the upper three leaves of 16 barley cultivars when exposed to yellow rust, *Puccinia striiformis* f. sp. *hordei*

Cultivar	Toluca-1				Toluca-2				Celaya			
	DS_m	DS_{60}	AUDPC	b^{-1}	DS_m	DS_{60}	AUDPC	b^{-1}	DS_m	DS_{60}	AUDPC	b^{-1}
Apizaco*	*98*	*37.3*	*2,854*	*6.2*	*99*	*39.4*	*2,387*	*4.8*	100	56.6	2,386	3.8
Guanajuato	96	61.3	2,160	6.8	83	53.8	1,662	4.4	92	65.9	1,804	3.0
Centinela	90	7.4	1,917	5.6	86	30.6	1,720	4.5	50	2.3	790	1.9
Arupo*	82	5.6	1,841	4.9	67	16.6	1,430	3.1	*76*	*32.3*	*1,484*	*2.7*
Cerro Prieto	87	29.0	2,047	6.1	75	33.8	1,499	3.8	83	51.4	1,434	2.6
Trompillo	83	49.1	2,205	7.2	81	49.3	1,818	4.7	92	67.4	1,870	3.1
Puebla	87	21.9	1,810	5.1	71	21.3	1,328	3.2	82	25.6	1,460	2.6
Klages	71	47.1	1,388	3.6	66	35.3	1,329	2.6	68	63.5	1,185	2.3
Esperanza	39	8.8	770	1.5	29	5.8	509	1.2	55	12.5	933	2.0
Esmeralda	39	5.8	702	1.6	36	6.3	535	1.8	53	10.8	811	1.9
Ase/3CM**	26	11.5	337	1.4	24	8.4	373	1.3	25	14.7	318	1.4
Granado	16	7.8	261	0.9	23	4.6	280	1.4	25	10.7	320	1.4
Gloria/Copal	11	2.0	147	1.0	13	3.7	204	0.9	13	6.0	186	1.0
Calicuchima-92	9	2.1	110	0.9	11	2.3	127	1.1	9	3.7	133	0.9
Maris/Mink**	6	0.8	89	0.6	16	2.2	198	1.2	13	1.6	188	1.1
Aleli	6	0.5	100	0.4	15	2.7	166	1.1	20	4.0	309	1.2

* The data in italics are missing values estimated from the real data but corrected for the experiment effects

** Advanced lines derived from complex crosses; Maris/Mink/Esc.II.72.83.3E.7E.5E.1E//Shyri and Ase/3CM//RO/3/Smai/4/Ruda''S''/5/Agave''S''

Table 3 Mean disease severity (DS) when the most susceptible cultivar reached its maximum DS (DS_m), mean DS when the cultivars were at plant stage 60 (DS_{60}), mean area under the disease progress curve (AUDPC), mean disease increase rate (b^{-1}) × 100, and mean infection type (IT) averaged over three experiments of the upper three leaves of 16 barley cultivars when exposed to yellow rust, *Puccinia striiformis* f. sp. *hordei*

Cultivar	DS_m	DS_{60}	AUDPC	b^{-1}	IT
Apizaco**	98.8 a*	44.4 bc*	2,542 a*	4.9 a*	8
Guanajuato	90.3 a	60.3 a	1,875 bc	4.7 a	7
Centinela	75.3 a	13.4 def	1,476 d	4.0 ab	8
Arupo***	75.0 a	18.2 de	1,585 bcd	3.6 ab	7
Cerro Prieto	81.7 a	38.1 c	1,660 bcd	4.2 ab	8
Trompillo	85.3 a	55.3 ab	1,964 b	5.0 a	8
Puebla	80.0 a	22.9 d	1,533 cd	3.6 ab	8
Klages	68.3 a	48.6 abc	1,301 d	2.8 bc	7
Esperanza	41.0 b	9.0 ef	737 e	1.6 cd	8
Esmeralda	42.7 b	7.6 ef	683 ef	1.8 cd	5
Ase/3CM****	25.0 bc	11.5 def	343 efg	1.4 d	8
Granado	21.3 bc	7.1 ef	287 g	1.2 d	8
Gloria/Copal	12.3 c	3.9 f	179 g	1.0 d	7
Calicuchima-92	9.7 c	2.7 f	123 g	1.0 d	7
Maris/Mink****	11.7 c	1.5 f	158 g	1.0 d	5
Aleli	13.7 c	2.4 f	192 g	0.9 d	5

* Significantly different according to Duncan's New Multiple Range Test at $P = 0.05$ if letters are different; ** was present in only one environment; *** was present in two environments

**** See Table 2

Table 4 Pearson linear correlation coefficients and Spearman rank correlation coefficients between four epidemiological parameters measured in the upper three leaves of barley cultivars affected by yellow rust

Parameter	Pearson			Spearman		
	DS_m	DS_{60}	AUDPC	DS_m	DS_{60}	AUDPC
DS_{60}	0.81			0.93		
AUDPC	0.99	0.83		0.98	0.88	
b^{-1}	0.97	0.83	0.98	0.97	0.92	0.96

All values highly significant, $P \leq 0.001$

Table 5 Pearson linear correlation coefficients and Spearman rank correlation coefficients between environments for four epidemiological parameters of barley cultivars affected by yellow rust

Environments	Pearson				Spearman			
	DS_m	DS_{60}	AUDPC	b^{-1}	DS_m	DS_{60}	AUDPC	b^{-1}
Tol1/Tol2	0.99	0.99	0.92	0.98	0.95	0.97	0.88	0.91
Tol1/Cel.	0.93	0.93	0.97	0.91	0.85	0.91	0.92	0.88
Tol2/Cel.	0.90	0.89	0.89	0.85	0.86	0.87	0.83	0.85

All values highly significant, $P \leq 0.001$

showed small but significant differences between some cultivars. The seedling disease severity (SDS) too showed small but significant cultivar differences (Table 6). ''Guanajuato'' had the lowest SDS (31%) and ''Arupo'' the highest (55%). The infection type (IT) was high in all cultivars and varied between 7 and 8. The SLP_{50} and the SDS were not correlated.

Table 6 Seedling latency period 50 (SLP_{50}) in days and relative to that of cv. Apizaco, set at 100% (Rel), mean seedling disease severity (SDS) and relative SDS to that of Apicazo set at 100% (Rel) and infection type (IT) caused by *P. striiformis* f. sp. *hordei* race 24 on 16 spring barley cultivars. Means of two experiments. Cultivars are ranked according to their latency period (LP_1) on the flag leaf (Table 7)

Cultivar	SLP_{50}[a]		SDS		IT
	Days	Rel	Mean	Rel	
Apicazo	9.0	100	48	100	8
Trompillo	8.8	98	36	74	8
Guanajuato	9.5	106	31	64	7
Cerro Prieto	8.7	97	43	89	8
Arupo	8.7	97	55	115	7
Ase/3CM*	8.6	96	45	94	8
Puebla	9.2	102	43	90	8
Klages	9.2	102	43	89	7
Centinela	9.5	106	47	98	8
Granado	9.4	104	47	98	8
Maris/Mink*	9.2	102	34	70	7
Esperanza	9.5	106	40	82	7
Alelí	9.1	101	47	97	7
Esmeralda	9.4	104	46	95	7
Gloria/Copal	9.1	101	45	94	7
Calicuchima-92	9.3	103	47	98	7
LSD 5%[b]	0.2	2	2	4	

* See Table 2

[a] Period between the start of incubation and sporulation in 50% of the seedlings

[b] Least significant difference at $P < 0.05$

Adult plant experiments

Latency period 1 (LP_1) and latency period 50 (LP_{50}) in the adult plant stage varied widely between cultivars (Table 7) and large, significant differences were observed on both the flag leaf (FL) and the leaf below the flag leaf (FL-1). On the FL, the LP_1 in ''Calicuchima-92'' was, on average, 11.7 days (93%) longer than the LP_1 in ''Apizaco'' and on FL-1 it was 8.9 days (60%) longer than the LP_1 in ''Apizaco''. On average, the LP_1 on FL-1 was 1.1 days longer than LP_1 assessed on FL (Table 7). There was a highly significant correlation between the values of LP1 for the FL and the FL-1 ($r = 0.95$).

On FL's, the LP_{50} was on average 55% longer on ''Calicuchima-92'' than on ''Apizaco''; a similar result was found for the FLs-1 (Table 7). On average, LP_{50} on FL-1 was 0.7 days longer than LP_{50} assessed on FL. The correlation coefficient between the LP_{50} for FL and for FL-1 was high and positive ($r = 0.94$).

Infection frequency

The spore counts on the greased slides in the settling tower next to the water agar pieces revealed very small differences between applied spore densities. The number of spores per cm^2 was 1,518, 1,522 and 1,519 for experiment 1, 2 and 3, respectively. The IF varied greatly between cultivars and significant cultivar differences were observed in both the FL and FL-1 (Table 8). In both the FL and the FL-1 three groups of cultivars could be discerned. ''Apizaco'' formed group 1 with a very high IF, 23.1 infections per cm in de FL and 14.3 in the FL-1. ''Trompillo'', ''Guanajuato'', ''Cerro Prieto'', ''Arupo'' and ''Ase/3CM'', with a clearly lower IF (15.1–8.5 for the FL and 7.1–3.4 for the FL-1), formed the second group. The remaining cultivars formed the third group with an IF ranging from 3.6 to 0.0 on the FL and from 2.5 to 0.0 on the FL-1. The IF on the FL-1 was on all cultivars lower than on the FL, except for ''Esmeralda'', with no infections at all on both leaves. The Spearman rank correlation coefficient between the IF's of the FL and those of the FL-1 was high and positive ($r = 0.96$).

Colonization rate

The CR varied significantly between cultivars for both the FL and FL-1 (Table 8), but the differences between cultivars were considerably smaller than for the IF. Remarkable was the high CR of ''Granado'', which had a very low IF. Several other cultivars with a low IF had a relatively high CR. Also remarkable was the clearly higher CR in the FL-1 compared with that in the FL, which is a reversal compared with that for the IF. There was a high correlation between the CR assessed on FL and the CR assessed on FL-1 ($r = 0.85$).

Infection type

In the seedling stage ITs among the cultivars ranged from 7 to 8, which is considered to be a susceptible reaction (Table 6). In the adult plant stage the IT ranged from 5 to 8. The cultivars

Table 7 Latency period 1 (LP_1) and latency period 50 (LP_{50}) in days and relative to that of cv. Apizaco set at 100% (Rel), measured on the flag leaf (FL) and leaf below the flag leaf (FL-1) of 16 spring barley cultivars, and their infection types (IT) after exposure to *P. striiformis* f. sp. *hordei* race 24. Cultivars are ranked according to their LP_1 on the flag leaf

Cultivar	LP_1, mean of three experiments				LP_{50}, mean of four experiments				IT
	FL		FL-1		FL		FL-1		
	Days	Rel	Days	Rel	Days	Rel	Days	Rel	
Apicazo	12.6	100	14.8	100	15.7	100	17.5	100	8
Trompillo	13.2	105	14.7	99	15.8	101	16.4	94	8
Guanajuato	14.3	113	15.7	106	16.2	103	17.7	101	7
Cerro Prieto	15.9	126	16.7	113	18.1	115	18.8	107	8
Arupo	16.8	133	18.6	126	18.7	119	19.6	112	7
Ase/3CM*	17.5	139	18.1	122	18.8	120	19.2	110	8
Puebla	18.3	145	18.9	128	20.3	129	19.8	113	8
Klages	18.5	147	20.0	135	19.7	125	21.6	123	7
Centinela	19.4	154	21.3	144	21.3	136	23.3	133	8
Granado	19.6	156	23.4	158	21.8	139	22.8	130	8
Maris/Mink*	20.2	160	20.4	138	22.2	141	21.8	125	5
Esperanza	21.8	173	23.0	155	22.0	140	–[b]	–[b]	8
Alelí	22.4	178	21.5	145	23.4	149	21.9	125	5
Esmeralda	23.5[a]	187[a]	–[b]	–[b]	–[b]	–[b]	–[b]	–[b]	5
Gloria/Copal	23.8	189	24.0	162	22.7	145	23.7	135	7
Calicuchima-92	24.3	193	23.7	160	24.4	155	26.0	149	7
LSD 5%[c]	3.5	28	3.0	20	4.2	27	3.9	22	

* See Table 2

[a] Was recorded only in one experiment

[b] Infection frequency was 0

[c] Least significant difference with $P \leq 0.05$

Maris/Mink, Alelí and Esmeralda had an IT of 5; for the other cultivars the IT did not change relative to the IT observed in the seedling stage (Table 7). On all cultivars the IT on FL was the same as on FL-1.

Associations between components

The correlation between the SLP_{50} and the adult plant resistance components LP_1, LP_{50} and IF were significant but not high, r being 0.5 (Table 9). With the CR the correlation was insignificant. The Seedling LP and DS showed no association with the quantitative resistance in the field as measured by the AUDPC and the DS_m.

The LP and the IF in the adult plant stage were very well correlated. The correlation of the CR with the LP and IF was inconsistent. The LP and the IF in the adult plant stage both had a fairly high correlation with the AUDPC and the DS_m, that of the LP being slightly higher than that of the IF. The CR did not correlate with the quantitative resistance in the field (Table 9).

To investigate the relative contribution of the three components for quantitative resistance multiple regression analyses were carried out. Table 10 shows the proportion of the variance of the quantitative resistance as measured by the AUDPC or the DS_m as explained by the components studied. The data indicate that the LP is the most important component and the CR the least. The data of the experiment Toluca-2 were left out as they gave too little extra information; they followed those of Toluca-1 very closely.

Discussion

Quantitative resistance to yellow rust in barley appears to be common. Sandoval-Islas et al. (1998) reported this for advanced lines in the ICARDA/CIMMYT breeding program. Also among

Table 8 Number of sporulating stripes per cm leaf width (IF) and the colonization rate in mm per day (CR) of *P. striiformis* f. sp. *hordei* race 24, measured on the flag leaf (FL) and the leaf below the flag leaf (FL-1) and the same values relative to those of cv. Apizaco set at 100% (Rel) of 16 spring barley cultivars. Mean of three experiments. Cultivars are ranked according to their mean LP_1 on the flag leaf (Table 7)

Cultivar	IF				CR			
	FL		FL-1		FL		FL-1	
	Mean	Rel	Mean	Rel	Mean	Rel	Mean	Rel
Apicazo	23.1	100	14.3	100	2.81	100	3.26	100
Trompillo	15.1	65	7.1	50	2.74	98	3.17	97
Guanajuato	10.4	45	5.0	35	2.55	91	2.76	85
Cerro Prieto	7.0	30	4.3	30	2.53	90	3.53	108
Arupo	11.0	48	3.4	24	1.48	53	2.86	88
Ase/3CM*	8.5	37	6.2	43	2.49	89	2.94	90
Puebla	2.6	11	1.1	8	2.34	83	3.00	92
Klages	2.5	11	1.5	10	1.41	50	1.63	50
Centinela	2.8	12	1.3	9	1.84	65	2.83	73
Granado	0.2	< 1	0.03	< 1	3.00	107	4.70	144
Maris/Mink*	3.6	16	2.5	17	1.56	56	1.21	37
Esperanza	0.01	< 1	0.0	0	0.30	11	–[a]	–[a]
Alelí	1.4	6	1.0	7	1.49	53	1.70	52
Esmeralda	0.0	0	0.0	0	–[a]	–[a]	–[a]	–[a]
Gloria/Copal	0.5	2	0.3	2	1.25	44	1.89	58
Calicuchima-92	1.1	5	0.5	3	1.44	51	1.90	58
LSD 5%[b]	–	–	–	–	1.40	50	1.73	53

[a] Infection frequency was 0

[b] Least significant difference with $P \leq 0.05$

* See Table 2

Table 9 Pearson linear correlation and Spearman rank correlation coefficients (in italics) between five components of quantitative resistance *to P. striiformis* f. sp. *hordei* measured on the flag leaf (FL) and leaf below the flag leaf (FL-1) of 16 barley cultivars, and three epidemiological parameters measured in the field in three environments

Components		LP_1^b	LP_{50}^c	IF[d]	CR[e]	AUDPC[f]	DS_m^g	b^{-1} [h]
SLP_{50}^a	FL	0.50*	0.48*	*–0.48**	–0.23[NS]	–0.25[NS]	–0.13[NS]	–0.25[NS]
	FL-1	0.52*	0.49*	*–0.42*[NS]	–0.13[NS]	–0.24[NS]	–0.24[NS]	–0.28[NS]
LP_1^b	FL		0.98**	*–0.87***	–0.70**	–0.75**	–0.75**	–0.83**
	FL-1		0.96**	*–0.87***	–0.32[NS]	–0.77**	–0.80**	–0.82**
LP_{50}^c	FL			*–0.83***	–0.63*	–0.77**	–0.78**	–0.83**
	FL-1			*–0.85***	–0.42[NS]	–0.71**	–0.74**	–0.74**
IF[d]	FL				*0.54***	*0.73***	*0.68***	*0.66***
	FL-1				*0.43*[NS]	*0.75***	*0.71***	*0.74***
CR[e]	FL					0.30[NS]	0.37[NS]	0.42[NS]
	FL-1					0.35[NS]	0.38[NS]	0.41[NS]

[a] Seedling latency period 50

[b, c, d, e] The latency period 1, the latency period 50, the infection frequency and the colonization rate observed on the flag leaf and flag leaf minus one, respectively

[f, g, h] The area under the disease progress curve, the disease severity (DS) when the most susceptible cultivar reached its maximum DS, and b^{-1}, an estimator of the rate of disease increase according to the Weibull model

** $P \leq 0.01$; * $P \leq 0.05$; [NS] = not significant

cultivars quantitative resistance it is far from rare as is shown by the research reported here. This is in agreement with the conclusion of Parlevliet (1993) that oligogenic or polygenic quantitative resistance is present at low to fair levels in most cultivars of nearly all crops to all important pathogens.

Table 10 Proportion of the variance of the area under the disease progress curve (AUDPC) and the disease severity measured when the most susceptible cultivar reached its maximum disease severity (DS_m) of *P. striiformis* f. sp. *hordei* development on 16 spring barley cultivars in two field experiments, explained by one, two or three components of quantitative resistance measured on the flag leaf and the flag leaf minus one

Epidemiological parameter	Exp.	Component[a]					
		LP_1	IF	CR	LP_1 + IF	LP_1 + CR	LP_1 + IF + CR
Flag leaf							
AUDPC	Toluca-1	0.56	0.41	0.05	0.56	0.66	0.67
DS_m	Toluca-1	0.53	0.29	0.06	0.55	0.60	0.67
AUDPC	Celaya	0.61	0.49	0.12	0.61	0.71	0.71
DS_m	Celaya	0.58	0.35	0.11	0.60	0.70	0.72
Leaf below flag leaf							
AUDPC	Toluca-1	0.55	0.22	0.11	0.72	0.57	0.74
DS_m	Toluca-1	0.51	0.20	0.10	0.69	0.54	0.71
AUDPC	Celaya	0.73	0.47	0.13	0.73	0.74	0.74
DS_m	Celaya	0.71	0.35	0.15	0.74	0.73	0.76
Mean		0.60	0.35	0.11	0.65	0.66	0.72

[a] LP1, IF and CR are, respectively, latency period 1, infection frequency and colonization rate

The cultivars with a susceptible IT in the adult plant stage represented at least five levels of quantitative resistance ranging from very susceptible to quite resistant (Table 3) suggesting an oligogenic or polygenic inheritance. This agrees with Sandoval-Islas et al. (2002), who concluded that the quantitative resistance in ''Calicuchima-92'', ''Gloria/Copal'' and ''Alelí'' was incompletely recessive and inherited in an oligogenic way. QTL analysis confirmed that a restricted number of QTLs can give a fairly high level of quantitative resistance. QTLs were found at chromosomes 4, 5 and 7 (Castro et al. 2003a, b). In the present study the quantitative resistance was expressed very well in all three environments, the cultivar × environment (G × E) interaction variance being very small compared to the very large cultivar variance (Table 1). This stable expression of quantitative resistance is also reported from other cereal–rust pathosystems. The partial resistance to wheat leaf rust, *P. triticina*, came to expression very well in widely different environments such as Mexico, Brazil, and The Netherlands (Broers and Parlevliet 1989). The partial resistance to barley leaf rust, *P. hordei*, too is very stable, being expressed very well in Western Europe, Morocco, Israel and Mexico (Parlevliet et al. 1988).

The covariance analysis did not indicate a significant effect of earliness on the DS_m. This is not surprising as the epidemics developed after all cultivars had developed their flag leaves. The differences in ranking between the DS_m and the DS_{60} do, however, suggest some effect of lateness on the DS (Tables 2, 3). Four of the quite resistant cultivars are late heading, while several of the susceptible cultivars are early heading. The association between later heading and higher levels of quantitative resistance in barley to yellow rust also exists to barley leaf rust (Parlevliet and Van Ommeren 1975).

To assess the DS accurately and reliably, various parameters, such as the DS_m, the AUDPC and the apparent infection rate have been used by various researchers (Parlevliet 1979; Kranz 1983; Steffenson and Webster 1992; Shaner 1996). The AUDPC is often considered the best parameter as it estimates the DS over the full period of exposure to the disease. Gaunt (1995) mentioned that single point models are only useful when the epidemic development is not too variable and occurs relatively late in the crop development. In this study the correlation between the AUDPC was very high with the DS_m and the disease increase rate, and fairly high with the DS_{60}. This high correlation is probably due to the rather late development, from ear emergence onward, of the epidemics in all three experiments. For selection purposes the DS_m is very suitable as the breeder needs a fast and reliable evaluation method. The AUDPC on the other hand is more suitable for scientific studies were accuracy is most important

and for environments were yellow rust develops early or irregularly. The parameters ''apparent infection rate'' and ''disease increase rate'' have the disadvantage of being less accurate than the AUDPC as they tend to harbour a larger error. Although the DS_{60} could be thought to be the better assessment method as it would take into account differences in heading date it has at the same time the disadvantage that the observations are taken at different moments, which may introduce another error. In this study it was the parameter that correlated less well with the other three parameters (Table 4).

The LP, IF and CR are important components of quantitative resistance (Mehta and Zadoks 1970; Parlevliet 1975, 1979; Parlevliet and Kuiper 1977; Broers 1989a, b; Habtu and Zadoks 1995; Broers 1997). In the seedling stage the differences in LP among cultivars were small. Osman-Ghani and Manners (1985), working with the same pathosystem, found similar results for winter barley. In the barley–barley leaf rust pathosystem Parlevliet (1975) and Parlevliet and Van Ommeren (1975) also observed small cultivar differences in LP in the seedling stage, while the LP in the flag leaf showed much larger differences between cultivars. The flag leaf LP was very highly correlated with the partial resistance in the field. In the wheat-leaf rust pathosystem the observations were very similar (Broers 1989a, b). Apparently quantitative resistance is expressed to a limited extent in the seedling stage. In this stage resistance is usually not necessary as the disease normally develops in later plant stages. In the adult plant stage the LP was much longer and the cultivar differences much larger than in the seedling stage, similar to the situation in the leaf rusts of barley and wheat as mentioned above. The LP is often considered to be a very important component of quantitative resistance. Zadoks (1971) and Teng et al. (1977) demonstrated that small changes in the LP can have a strong impact on the development of rust epidemics. The IF showed large differences among cultivars. Similar results have been found in several other pathosystems (Parlevliet and Kuiper 1977; Ahn and Ou 1982; Groth and Urs 1982; Broers 1989a, b).

The CR is a more complex component. The growth of rust infections is density dependent. In bean rust the growth rate of uredosori and spore production were negatively associated with infection density (Yarwood 1961). In wheat leaf rust (Mehta and Zadoks 1970) and barley leaf rust the same was observed (Baart et al. 1991). This density depending effect starts as soon as the much energy asking spore production starts. In the initial period of infection, before the spore production starts, there is no effect of the infection density on the growth of the colonies (Baart et al. 1991). The density effect is strong and it probably played a role here too. The differences in IF between cultivars was large and as a consequence affected the cultivar effects on CR considerably, resulting in fairly high CR's for the cultivars with a very low IF. This also explains its low correlation with the AUDPC and the DS_m. The CR is therefore most likely not an independent component of resistance. As a consequence, assessing it accurately is very difficult and estimating its effect on quantitative resistance seems hardly possible.

The component long LP was best expressed in the flag leaf, the component low IF in the leaf below it. This reverse effect may be explained by the difference in age of the two leaves, the flag leaf being younger than the leaf below it. Parlevliet (1975) found that the LP of all barley cultivars decreased with increasing age of the leaves. This was not observed with the IF (Parlevliet and Kuiper 1977).

Within many plant–pathogen systems, association between components of quantitative resistance have been reported, although the degree of association can vary considerably (Parlevliet 1992). The barley–yellow rust pathosystem is no exception. The LP and the IF in the adult plant stage are mutually correlated and correlated well with the quantitative resistance as measured by the DS_m and the AUDPC. The quantitative resistance in three of the cultivars investigated here appeared to be controlled by two or three genes (Sandoval et al. 2002). The strong association between the LP and IF is suggestive for a control of both components by these two or three genes.

Of the three components investigated, the variance in the LP contributed most, 60%, the variance in the IF less, 35%, and the variance in the CR little, 11%, to the quantitative resistance

(Table 10). As mentioned above, the contribution of CR is probably underestimated due to its negative association with IF.

It can be concluded that quantitative resistance can be assessed very well in the field. Due to its common occurrence selection for higher levels of quantitative resistance should not be difficult.

Acknowledgements This research was partly financed by the Dutch Minister for Development Cooperation (DGIS/DST/SO), Colegio de Postgraduados and Consejo Nacional de Ciencia y Tecnología de México (CONACYT) as a part of a collaborative project between the International Maize and Wheat Improvement Center (CIMMYT) in Mexico and the Department of Plant Breeding of the Wageningen Agricultural University (WAU). We thank Diego González de Leon for critical reading and Rosa Atilano for technical assistance.

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