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Combining Ability Analysis of Fusarium Head Blight Resistance in European Winter Wheat Varieties

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The aims of the present study were to estimate the general combining ability (GCA) and the specific combining ability (SCA) effects controlling type II FHB resistance across environments in a set of European winter wheat varieties and, for purposes of future selection, to identify potential combinations of parents with suitable levels of FHB resistance. Parental varieties as well as F_1 generations were evaluated under both field and greenhouse conditions in two years. The results of the present study indicate that in the F_1 generation mean DON content was relatively lowest after crossing of moderately resistant parents (Sakura/Bakfis, Sakura/Federer, Petrus/Bakfis, and Sakura/Petrus), and mean DON content is low also after crossing the moderately resistant Bakfis variety with the susceptible Biscay and Cubus varieties. Evaluation of crosses in the F_1 generation was followed by evaluation of selected crosses (derived from the Bakfis and Sakura varieties) in the F_2 generation. Correlations between F_1 and F_2 were highly significant in relation both to their DON content and visual symptom score (VSS), as well as between the individual experiments (and in the different years). The only exception was in the case of the 2014 field experiment, when inoculation was successful but conditions were not optimal for the disease to progress and DON to accumulate. The selection of a suitable parental variety (with a high GCA) can markedly influence the success rate of breeding for resistance to FHB. Detection of high SCA in the F_1 generation is important for directing breeders to promising combinations for achieving FHB resistance. It was demonstrated here that low DON content may be achieved even after crossing a moderately resistant variety with susceptible varieties. Another possibility is to make use of heterosis directly for acquiring resistance in hybrid wheat (for decreasing DON content and manifestation of symptoms).

Keywords: common wheat, DON content, *Fusarium culmorum*, combining ability, heterosis

Abbreviations: FHB: Fusarium head blight, GCA: General combining ability, SCA: Specific combining ability, DON: mycotoxin deoxynivalenol

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Introduction

Fusarium head blight (FHB) is one of the most damaging diseases in small-grain cereals, and particularly in years with intensive rainfall. FHB resistance is polygenic, and its expression is highly influenced by the environment. Resistance to FHB in small grain cereals is inherited predominantly as a quantitative trait in an additive-dominance model (Bai et al. 2000; Jiang and Ward 2006). In susceptible cultivars, the predisposition to produce the mycotoxin deoxynivalenol (DON) is of key importance, but in highly resistant cultivars resistance is the major factor in suppressing disease development and DON accumulation (Mesterházy 2002). Environmental conditions play a crucial role in FHB's development in wheat, and variation in FHB symptom expression due to environmental interactions remains a major challenge in terms of accurately assessing FHB resistance.

Resistance breeding is the most effective and elegant way to control for FHB, which causes yield losses and leads to contamination of feed and foodstuffs by harmful mycotoxins (Becher et al. 2013). It was demonstrated by Šíp et al. (2007) that moderate resistance in combination with fungicide treatment may result in reducing DON by as much as 89% (while reducing pathogen DNA content by as much as 96%).

Because it is believed that appropriately utilizing sources of even moderate resistance can accelerate the development of wheat cultivars resistant to FHB, more attention should undoubtedly be given to identifying parental combinations with suitable levels of FHB resistance (Zwart et al. 2008). Single-cross prediction based on mid-parent performance shows promise for simple and highly heritable traits, but its use is hampered for more complex traits due to a masking by dominance effects (Smith 1986; Oettler et al. 2005). Mid-parent performance could serve as a moderate indicator for FHB resistance in single-cross triticale hybrids (Boeven et al. 2016). Statistically significant effects for both general combining ability (GCA) and specific combining ability (SCA) in diallels of winter wheat have been reported in point inoculation trials with *F. graminearum* (Hall and Van Sanford 2003) and spray inoculation trials with *F. culmorum* (Buerstmayr et al. 1999).

The aims of the present study were to estimate the GCA and SCA effects controlling type II FHB resistance across environments in a set of European winter wheat varieties and, for purposes of future selection, to identify potential combinations of parents with suitable levels of FHB resistance.

Material and Methods

Eight winter wheat varieties were crossed in all possible pairwise combinations and without reciprocals to produce 28 F_1 lines. The parental genotypes were chosen on the basis of their overall resistance to FHB (Chrpová et al. 2012). The parental winter wheat varieties (Table S1*) are currently listed in the Czech National List (http://eagri.cz/public/app/sok/odrudyNouQF.do?lang=en_US). The variety 'Petrus' was also included as parent in the diallel because it is a well-characterized source of FHB resistance in western Euro-

*Further details about the Electronic Supplementary Material (ESM) can be found at the end of the article.

pean winter wheat that could be of great value in European breeding programmes (Gosman et al. 2007).

The resistance levels of the parents and F_1 crosses were evaluated in two years (2013 and 2014) and in two environments (field and greenhouse). Thus, there were four experiments altogether.

The parents and F_1 crosses were planted in hill plots in three replications in field conditions and also in sheltered boxes (unheated greenhouses). Spikes were artificially inoculated using highly pathogenic isolate B of *Fusarium culmorum* (Šíp et al. 2002) at the phase of full flowering (BBCH 65). Inoculum (conidial suspension $0.8 \times 10^7/\text{ml}$) was sprayed one time onto bunches of 5 flowering spikes randomly selected within hill plots. Inoculation dates for individual varieties or F_1 crosses differed according to their flowering times.

Inoculated spikes were then kept in polythene bags for 24 h. To minimize year and location effects on results, it appeared necessary in these conditions to support disease development (as appropriate) by irrigating plots. *Fusarium* head blight symptoms (expressed as percentage of spikelets displaying such symptoms) were evaluated for three time periods (14, 21 and 28 days after inoculation). Seeds from infected spikes were analysed for DON content as determined by ELISA using RIDASCREEN®FAST DON kits from R-Biopharm GmbH, Darmstadt, Germany. DON content determination is described in detail by Chrpová et al. (2007).

F_2 progenies derived from the varieties Bakfis and Sakura were also evaluated in field trials during 2014 and 2015. Plants of the F_2 generation were grown on row plots 1 m long (plant spacing: 6×22 cm). The spore mixture ($0.8 \times 10^7 \text{ ml}^{-1}$) was applied at a rate of approximately 150 ml/m^2 onto the heads using a hand sprayer on two dates: at full flowering (>50% of flowering spikes) and 1 week later. The resistance level of each F_2 cross was evaluated as the percentage of plants having low-level FHB symptoms (VSS on levels 1, 2, and 3 of scale 1–9, 1 without symptoms), the average symptom score for each cross, and the DON content in randomly selected plants.

The UNISTAT 6.5 package (UNISTAT Ltd., London, UK) was used for statistical analyses. Analysis of variance (ANOVA) for individual environments (field and greenhouse) and across environments was performed to determine the sources of variation for percentage of FHB symptoms and DON content. Least-square means, based on a general linear model were used to estimate GCA and SCA effects of the F_1 crosses across environments according to Griffing's (1956) experimental model 1.

Results

Parental varieties as well as F_1 generations were evaluated under both field and greenhouse conditions in two years (2013 and 2014). Mean DON content and visual symptom score (VSS), representing the percentage of FHB spread, of the parental varieties are presented in Table 1. In evaluating the F_1 generation, a strong negative heterosis effect was determined as compared to the mean for the parents (Table 2). The mean difference between real and expected DON content was -20.8 mg/kg and that for spike infection

Table 1. Mean DON content and symptom score of parental varieties in the individual experiments

Parent	DON content (mg/kg)			
	Field 2013	Field 2014	Greenhouse 2013	Greenhouse 2014
Bakfis	20.02	33.72	25.89	17.26
Biscay	273.05	103.73	99.87	124.08
Bohemia	89.23	53.60	49.72	42.27
Cubus	136.11	23.23	108.37	80.58
Elly	127.60	64.82	47.30	36.63
Federer	32.02	34.03	66.61	78.18
Petrus	43.55	26.78	104.73	93.66
Sakura	43.92	11.63	59.72	21.91
Mean	95.69	43.94	70.27	61.82
	% FHB spread			
Bakfis	26.67	16.89	29.00	11.22
Biscay	67.78	52.22	51.67	56.44
Bohemia	40.00	10.78	26.44	5.56
Cubus	55.56	5.78	46.44	43.78
Elly	47.78	28.67	55.56	16.22
Federer	20.11	18.33	25.22	18.78
Petrus	20.00	4.56	32.22	18.22
Sakura	24.11	8.22	18.78	9.00
Mean	37.75	18.18	35.67	22.40

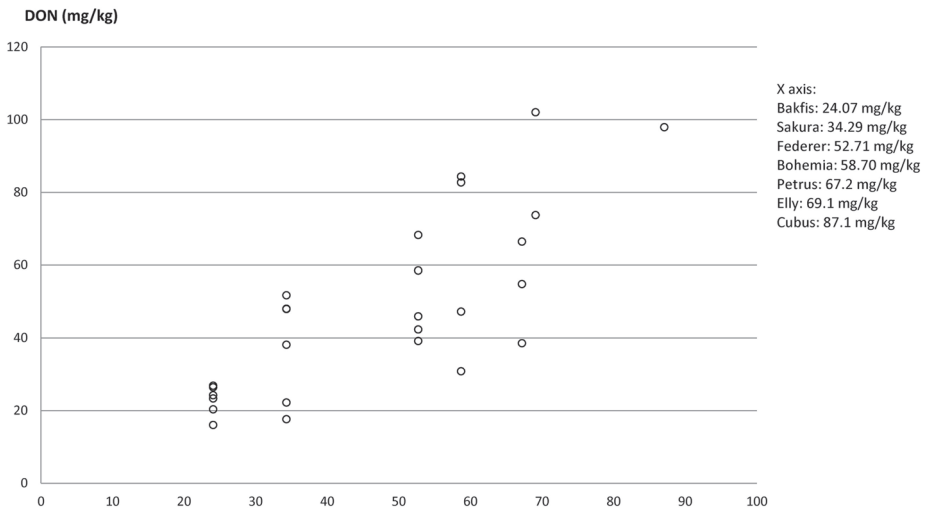


Figure 1. Comparing actual DON content (mg/kg) of the cross to DON content of the better parent (x axis)

Table 2. Heterosis of F₁ generation crosses relative to the parents' average (MP) and to the "Better-more resistant" parent (BP) for DON content and spike infection (SH); mean values from four experiments from 2013 and 2014

Crosses		DON (mg/kg)	MP	BP	% FHB spread	MP	BP
Sakura	Bakfis	16.0	-13.2	-8.1	8.8	-9.2	-6.3
Sakura	Federer	17.6	-25.9	-16.7	12.2	-5.6	-2.8
Petrus	Bakfis	20.3	-25.4	-3.8	7.5	-12.3	-11.2
Sakura	Petrus	22.2	-28.6	-12.1	9.1	-7.8	-5.9
Bakfis	Elly	23.3	-23.2	-0.7	13.9	-15.1	-7.1
Cubus	Bakfis	24.2	-31.4	0.1	9.7	-19.7	-11.3
Bakfis	Biscay	26.0	-61.1	2.0	12.4	-26.6	-8.5
Federer	Bakfis	26.4	-12.0	2.4	10.3	-10.5	-10.3
Bakfis	Bohemia	26.8	-14.6	2.7	12.3	-8.5	-8.4
Petrus	Bohemia	30.8	-32.1	-27.9	8.6	-11.1	-10.1
Sakura	Bohemia	38.1	-8.4	3.8	16.4	-1.4	1.4
Petrus	Elly	38.5	-29.6	-28.7	13.7	-14.2	-5.0
Federer	Bohemia	39.1	-16.6	-13.6	14.1	-6.5	-6.5
Federer	Elly	42.3	-18.6	-10.4	23.8	-5.1	3.2
Federer	Petrus	45.9	-14.1	-6.9	12.8	-6.9	-6.0
Bohemia	Elly	47.5	-16.4	-11.2	21.9	-7.0	1.2
Sakura	Elly	47.9	-3.8	13.6	13.8	-12.2	-1.2
Cubus	Sakura	48.0	-12.7	13.7	20.3	-6.2	5.2
Sakura	Biscay	51.7	-40.6	17.4	21.9	-14.1	6.9
Petrus	Biscay	54.8	-53.8	-12.3	17.4	-20.5	-1.4
Federer	Cubus	58.5	-11.4	5.8	22.8	-6.5	2.1
Petrus	Cubus	66.4	-10.8	-0.8	22.5	-5.8	3.8
Federer	Biscay	68.2	-33.2	15.5	24.5	-14.3	3.9
Cubus	Elly	73.7	-4.4	4.6	24.8	-12.7	-12.3
Biscay	Bohemia	82.7	-21.7	24.0	28.5	-10.3	7.9
Cubus	Bohemia	84.3	11.5	25.6	28.6	-0.7	7.9
Cubus	Biscay	97.9	-20.8	10.8	28.6	-18.8	-9.3
Biscay	Elly	102.0	-7.7	32.9	30.6	-16.5	-6.5
Average		47.2	-20.8	1.8	17.6	-10.9	-3.1

The values of general combining ability (GCA) for DON content and FHB spread (%) are in bold

Table 3. Estimates of combining abilities for DON content (mg/kg) and symptom score (% FHB spread); estimates of specific combining abilities of crosses for DON content are above the diagonal line, for symptom score under the diagonal line; means from four experiments in 2013 and 2014

Parent	Specific combining ability (SCA)							
	Bakfis	Sakura	Petrus	Federer	Bohemia	Elly	Cubus	Biscay
Bakfis (MR)	x	5.2	4.1	6.1	0.6	-6.6	-18.7*	-20.5*
Sakura (MR)	1.0	x	-5.2	-14.0	0.7	6.8	-6.1	-6.0
Petrus (MR)	1.3	-1.1	x	9.0	-12.0*	-8.0	7.0	-8.2
Federer (M)	-0.1	-2.1	0.0	x	-7.9**	-8.4*	2.3	3.62
Bohemia (MS)	0.5	0.7	-5.6*	-4.2	x	-9.5	14.9	9.6
Elly (M)	0.4	-3.7	-2.2	3.8*	0.4	x	0.5	25.2*
Cubus (S)	-6.1*	0.5	4.3*	0.4	4.8	-0.7	x	13.4
Biscay (S)	-4.4**	1.2	-1.8	1.2	3.9	4.1	1.3	x

Parent	General combining ability (GCA)			Average of parents		
	DON content	% FHB spread	DON content	% FHB spread	DON content	% FHB spread
Bakfis (MR)	-23.7**	-6.9**	24.1	20.9	24.1	20.9
Sakura (MR)	-12.5**	-2.9	34.3	15.0	34.3	15.0
Petrus (MR)	-7.1	-4.4*	67.2	18.8	67.2	18.8
Federer (M)	-3.0	-0.3	52.7	20.6	52.7	20.6
Bohemia (MS)	3.0	1.1	58.7	20.7	58.7	20.7
Elly (M)	6.7	2.8	69.1	37.1	69.1	37.1
Cubus (S)	19.6**	5.1*	87.1	37.9	87.1	37.9
Biscay (S)	23.2**	6.1**	150.2	57.0	150.2	57.0
Average			67.9	28.5	67.9	28.5

* $P < 0.05$; ** $P < 0.01$

MR = moderately resistant, M = medium responsive, MS = medium susceptible, S = susceptible. The values of general combining ability (GCA) for DON content and FHB spread (%) are in bold.

Table 4. Correlation coefficients (*r*) between SCAs of the individual experiments (Field 2013 and 2014 and Greenhouse 2013 and 2014) for symptom score (% FHB spread) and DON content (*n* = 28)

% FHB spread	Mean		Field	2013	Field	2014	Greenhouse	2013
	<i>r</i>	P	<i>r</i>	P	<i>r</i>	P	<i>r</i>	P
Field 2013	0.640	0.0001						
Field 2014	0.373	0.0254	0.052	0.3966				
Greenhouse 2013	0.714	0.0000	0.364	0.0285	-0.184	0.1742		
Greenhouse 2014	0.582	0.0006	0.045	0.4110	-0.130	0.2553	0.530	0.0018
DON	Mean		Field	2013	Field	2014	Greenhouse	2013
	<i>r</i>	P	<i>r</i>	P	<i>r</i>	P	<i>r</i>	P
Field 2013	0.668	0.0001						
Field 2014	0.374	0.0249	-0.018	0.4630				
Greenhouse 2013	0.887	0.0000	0.497	0.0036	0.101	0.3047		
Greenhouse 2014	0.621	0.0002	0.240	0.1096	0.015	0.4704	0.496	0.0036

Note: Correlation coefficients are in bold.

-10.9%. The determined DON content was lower than the expected DON (parents' mean) in all cases other than one, that exception being the Cubus/Bohemia cross. The largest differences between the real and expected DON content and the real and expected spike infection were determined in the Bakfis/Biscay (-61.1/-26.6) and Petrus/Biscay (-53.8/-20.5) crosses. The Petrus/Biscay cross, however, exhibited almost double the DON content as compared to the Bakfis/Biscay cross. Figure 1 indicates a balanced low DON content in crosses with the Bakfis variety (point 24.1 mg/kg on the x axis) and considerably greater variability of DON content in crosses with the similarly moderately resistant varieties Sakura, Federer, and Petrus. DON content in all seven crosses with the Bakfis variety were in the range 16.0-26.8 mg/kg (overall mean for the crosses was 47.2 mg/kg). This finding can be considered very serious and it was supported, too, by the results of the combining abilities analyses (Table 3). GCA was the highest for DON content and visual symptom score, and it was highly significant in the Bakfis variety (-23.7**; -6.9**). The Sakura variety demonstrated a significant general effect only on decreasing the DON content, while that was true of the Petrus variety on decreasing the spike infection percentage. Significant effects on increasing DON content and spike infection were also demonstrated in the susceptible varieties Cubus and Biscay. SCA was significant in the cross of the Bakfis variety with the susceptible Cubus variety, and it was highly significant in its cross with the susceptible Biscay variety. It is also apparent that not every crossing of resistant parents will necessarily bring the expected effect. In evaluating heterosis of crosses in comparison to the "Better - more resistant" parent (BP), it was determined that crossing the Sakura and Federer varieties led to a significant decrease in DON content. Meanwhile, crossing Federer with Bakfis demonstrated an increase in DON content (Table 2). Statistical significance of specific effects from crosses on both DON content and spike infection were seen only infrequently, however, with that apparently being

Table 5. Evaluating crosses in the F₂ generation

F ₂ crosses	DON content (mg/kg)		Variance	Quadratic mean	Skewness	Kurtosis	Visual symptom score (VSS) on scale of 1-9; 1 without symptoms	
	Mean of two years	Median					Mean of two years	% of plants with higher resistance level (1, 2, 3)
Petrus/Bakfis	1.21	0.02	1.38	1.41	1.31	1.12	2.4	55
Sakura/Bakfis	1.66	0.27	1.66	1.55	1.34	0.54	2.4	55
Cubus/Bakfis	2.52	0.26	4.42	2.39	1.57	0.97	3.4	40
Federer/Bakfis	2.75	1.16	3.88	2.73	0.69	-0.99	3.0	42.5
Sakura/Petrus	3.10	0.41	6.06	3.06	1.13	0.33	2.7	47.5
Bakfis/Elly	3.52	0.49	3.31	2.26	1.83	3.64	2.7	47.5
Sakura/Federer	3.63	1.34	7.86	3.97	0.80	-0.04	3.7	30
Cubus/Sakura	4.80	3.80	9.80	4.48	0.37	-1.13	4.3	20
Bakfis/Biscay	6.29	4.33	13.19	6.16	0.35	-0.77	3.5	32.5
Federer/Elly	6.54	1.31	40.43	7.88	1.41	1.92	4.4	20
Bakfis/Bohemia	6.74	5.39	27.61	7.79	1.95	4.96	3.6	22.5
Sakura/Elly	7.97	3.07	26.48	6.95	1.37	0.19	3.7	27.5
Sakura/Bohemia	8.64	4.56	71.62	11.36	1.99	4.55	3.5	27.5
Sakura/Biscay	10.25	5.41	36.01	9.60	0.64	-0.73	4.3	22.5
Cubus/Biscay	10.53	10.28	44.19	12.05	0.18	-0.88	5.2	17.5

due to differences in symptoms of infection between various experiments (in different environmental conditions), as documented by the correlation analysis (Table 4).

According to the mean evaluation, the best conditions were those of the experiments “Greenhouse 2013”, “Field 2013”, as well as “Greenhouse 2014” ($r = 0.58\text{--}0.89$; $P < 0.001$), while the conditions of Field 2014 were the least suitable (Table 4). SCA estimates in experiments “Field 2014” were not correlated significantly with the estimates obtained from the other experiments. The “Field 2014” experiment produced both the relatively lowest DON content (36.5 mg/kg; overall mean = 51.7 mg/kg) and spike infection (12.5%; overall mean = 20.0%).

Evaluation of crosses in the F_1 generation was followed by evaluation of selected crosses (derived from the Bakfis and Sakura varieties) in the F_2 generation (Table 5). This was performed in 2014 and then repeated in 2015. In evaluating the progeny in the F_2 generation, highly significant correlation was determined between evaluations in the F_1 and F_2 generations both for DON content ($r = 0.7803$) and for visual symptom score ($r = 0.7856$) as well as between the individual experiments (and also in different years). The sole exception here was seen for the F_1 2014 field experiment. The experiments have confirmed the importance of evaluation already in the F_1 generation. Visual symptom score in F_1 correlated very well ($r = 0.8008$) with the percentage of resistant plants in the F_2 generation (VSS on levels 1, 2, and 3 of scale 1–9). Further information on combining abilities of parental varieties was provided by statistical evaluation of crosses in the F_2 generation. The low medians determined in the Petrus/Bakfis and Cubus/Bakfis combinations ensure a high proportion of resistant material in the hybrid generation. Evaluations of skewness and kurtosis also have informative value. Skewness indicates the extent to which values are symmetrically distributed around the selected central value or whether the distributed of the values is skewed to one side or the other (as were the cases for Bakfis/Bohemia and Sakura/Bohemia). Kurtosis indicates the shape of the probability distribution in relation to the central value. The higher the kurtosis in a distribution, the more tightly the values are concentrated around the central value.

Discussion

For selected parents, a hypothesis was verified that the level of resistance to Fusarium head blight can be detected on the basis of evaluation of symptomatic manifestation and content of the DON mycotoxin in early generations after the cross process (especially in F_1 and F_2). The seriousness of assessment of specific combination abilities is justified especially through the significantly different application of parent varieties and still rather negative experience during the use of remote forms with high resistance (e.g. Sumai3) in the breeding process (Kosová et al. 2009). A prospective strategy in the breeding of wheat seems to be the use of the varieties adapted to European conditions – Ittu et al. (2002). The data concerning the level of resistance to Fusarium head blight of these varieties is, however, many times insufficient. A possible solution is represented by determination of the general combination ability and specific combination ability, which enables identification of better parent lines (Hallauer et al. 2010).

The experiments reached methodological conclusions useful in breeding for resistance to FHB and in agricultural practice.

In evaluating the F_1 generation, a strong negative heterosis effect was determined as compared to the mean for the parent. This finding appears to be prospective for both classical breeding focused on creation of line varieties and for direct use of the heterosis effect for hybrid wheat (reduction of the DON content as well as of symptomatic manifestation). Heterosis is generally manifested in the form of larger performance and lifetime of the F_1 generation hybrids, arising through the cross process of suitably combining parent forms. The heterosis effect detection is a significant finding in the case of characteristics associated with resistance to *Fusarium* head blight. Similar conclusions were derived also by other studies, when it was found out that even where parental material is moderately susceptible, anecdotal evidence suggests that transgressive segregation may be an important factor in FHB-resistance breeding as evidenced by three widely used varieties, Ernie, Sumai3, and Truman, each of which was derived from moderately susceptible parents (McKendry et al. 1995, 2005; Bai et al. 2000). In that study it was evidenced that the low content of DON can be achieved even after the cross process of the susceptible variety with a moderately resistant variety (Cubus/Bakfis).

A statistically significant correlation between evaluations in the F_1 and F_2 generations for the two characteristics monitored (symptom score, DON content) confirms the importance of the evaluation of resistance to *Fusarium* head blight in the F_1 generation. Also, estimations of the general combination ability and specific combination ability were positively reflected in the parameters discovered in the splitting F_2 generation. In the F_2 generation, like in the F_1 generation, the series of crossbreds with the Bakfis variety stated, on average, a significantly lower DON content and higher % of resistant plants according to symptomatic evaluation, compared to the series of crossbreds with the Sakura variety featuring a similar slight resistance. The revealing of the specific combination ability highly depends, without any doubt, on exactness of determination of the level of resistance at parent varieties. As far as our experiments are concerned, an exceptional position was achieved especially by the Cubus (susceptible)/Bakfis (resistant) crossbred which stated, in the experiments held in 2013 even the lowest average DON content – exceptional characteristics (low median, etc.) were demonstrated also in F_2 .

While evaluating resistance to *Fusarium* head blight, it is necessary to establish suitable conditions for disease development (with the use of irrigation, or in the controlled environment). In this study it was found out that the results of 2014 from field conditions, when the lowest DON content as well as the lowest spike infection were achieved, differed from the other results. The reason was formed of worse conditions for disease development and DON accumulation. The interaction of the genotype with the environment in relation to manifestations of resistance to *Fusarium* head blight was described in a number of studies (Mesterházy 1995; Miedaner et al. 2001; Zwart et al. 2008).

Evaluation of resistance to *Fusarium* head blight in the F_1 or F_2 generations is not commonly carried out in the breeding practice. The reason is especially shortage of seeds in early generations as well as work demands. The results obtained indicate that the use of this method has its substantiation and it is suitable especially during the cross process of

parent varieties with an unknown level of resistance, where it is possible to obtain, on the basis of the results of evaluation of resistance in the F₁ generation, an idea of prospects of this combination from the viewpoint of resistance to *Fusarium* head blight. Another possibility is to make use of heterosis directly for acquiring resistance in hybrid wheat.

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Electronic Supplementary Material (ESM)

Electronic Supplementary Material (ESM) associated with this article can be found at the website of CRC at <http://www.akademiai.com/content/120427/>

Electronic Supplementary *Table S1*. Variety name, breeding company, pedigree and Fusarium head blight (FHB) resistance score of the eight European winter wheat varieties used as parents in the half-diallel