Response to selection in F_2 generations of winter wheat for resistance to head blight caused by *Fusarium culmorum*

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Summary

In a field trial, F_3 winter wheat lines from plants selected for Fusarium head blight resistance in F_2 generations of a set of crosses, composing a 10 × 10 half diallel, were tested with their parental lines for resistance to *Fusarium culmorum*. Selection responses averaged 3.7% on the head blight percentage scale and ranged from − 22.0% to 27.1%. Realized heritabilities averaged 0.23 and ranged from 0 to 0.96. Significant transgression for resistance was observed which was suggested to be genetically fixed. It was estimated that resistant parents differed in one or two resistance genes. The possibility of accumulation of resistance genes was shown. The level of head blight resistance of the parental line appeared to be a good indicator of the potential resistance level of its crosses.

Introduction

In bread wheat (*Triticum aestivum* L.), head blight caused by *Fusarium* spp. is a serious problem in many countries with a temperate climate (Nelson et al., 1981; Wang & Miller, 1987). In spite of efforts during the last few decades to breed wheat resistant to Fusarium head blight, progress has been slow. This is in part due to the lack of knowledge of the inheritance of the resistance. This report is one part of a study which was initiated to investigate the inheritance of the resistance to *Fusarium culmorum* (W.G. Smith) in winter wheat (Snijders, 1990a; 1990b).

Snijders (1990b) concluded from F_1 and F_2 analyses that resistance to head blight caused by *F. culmorum* in winter wheat was inherited predominantly in an additive way, although dominance effects were observed. Transgression occurred in some cases. The resistant parents differed in resist-

ance genes, but the data were insufficient to determine the number of genes. In the present study the response to selection and transgression for resistance were studied. An attempt was made to estimate the number of resistance genes in which the resistant parents differed.

Materials and methods

Plant material

In a field trial in 1988 the F_2 generations of a set of crosses, composing a 10 × 10 half diallel of winter wheat lines, were inoculated twice with *Fusarium culmorum* strain IPO 39-01 (Snijders, 1990a). Incidence of head blight was assessed on a single plant basis as the percentage infected spikelets of three inoculated heads. A selection of 110 resistant plants out of 1951 F_2 plants (5.6%) was obtained by

truncation selection. Truncation occurred at 10% head blight 21 days after first inoculation and at 25% head blight 28 days after first inoculation.

In a 1989 field trial, the 110 F_3 lines derived from the selected plants and the ten parental lines were tested for head blight resistance. The trial included three plots of each parental line consisting of up to 30 plants and one plot of each F_3 line consisting of up to 50 plants. The plots were randomized over the field. January 12, 1989, seeds were sown 0.12 m apart in rows 0.35 m apart, with no more than 10 seeds per row. As the seeds were harvested in 1988 from inoculated plots, all seeds were treated with methylmercury according to practice to prevent a seed-borne *Fusarium* infection.

Inoculation and disease assessment

For inoculation one pathogenic strain of *Fusarium culmorum* (IPO 39-01) was used and produced as described in Snijders & Van Eeuwijk (1990). Since wheat is most susceptible to infection at anthesis (Schroeder & Christensen, 1963), experimental inoculations were as far as possible carried out at this time. The heads of all plants of a plot were inoculated at the time when 50% of the plants within the plot were flowering. Inoculation was repeated after five days. The inoculum was sprayed with a propane spray-gun from 0.25 m above the crop at 250,000 spores/ml, in an amount of 1 L/10 m^2. A regular mist irrigation above the crop maintained a high relative humidity during the period June 14 to July 9. Incidence of head blight, expressed as the percentage of infected spikelets in the heads of the primary stem and primary tillers, was recorded on a single plant basis 21 days and 28 days after first inoculation (OBS-1 and OBS-2, respectively). Symptoms were described in Snijders & Perkowski (1990). Time of anthesis was recorded on a single plant basis.

Statistical and genetic analyses

Data on head blight were analyzed on a single plant basis. The weighted within-plot variance $\bar{\sigma}^2_{ew}$ was estimated from σ^2_{ew} of the homozygous parents, taking as weight the reciprocals of the standard error of the within plot mean square for each parent (Snijders, 1990b). The selection differential (S) was calculated as the difference in the mean head blight rating of the original F_2 population ($\bar{p}$) and that of the selected sample of resistant plants ($\bar{p}'$). The response to selection (R) was calculated as the difference between ($\bar{p}$) and the mean head blight rating of the progeny of the selected plants based on line means ($\bar{p}_1$). The realized heritability h^2_r was estimated by $h^2_r = R/S$.

Results

Due to differences in time of anthesis among F_3 lines and parental lines, the inoculation period lasted from June 14 to June 26. For the 2638 plants observed, the correlation coefficient between the date of first inoculation and Fusarium head blight rating was 0.39, and the correlation coefficient between the period between anthesis and first inoculation and Fusarium head blight rating was 0.34. The low correlations coefficients lead to the conclusion that although the inoculation time was chosen in accordance with the average time of anthesis per plot and not per plant, escape from infection was not likely.

The number of plants tested per parental line and per F_3 line averaged 64 and 18, respectively. The mean head blight incidence over all plants was 8.2% for OBS-1 and 29.0% for OBS-2. The correlation coefficient between OBS-1 and OBS-2 was 0.74. OBS-2, the head blight ratings assessed 28 days after first inoculation, showed larger differences in resistance among parental lines than OBS-1 and were comparable with the mean head blight ratings of the parental lines assessed in 1988 (Snijders, 1990b). Therefore, from here on only OBS-2 ratings for head blight are considered. In Fig. 1 the mean levels of head blight resistance of the parental lines of the 1989 trial are shown together with those of the 1988 trial where selection had taken place. Although the most susceptible genotypes had a lower head blight rating in 1989 than in 1988, levels of resistance of the parental lines in the
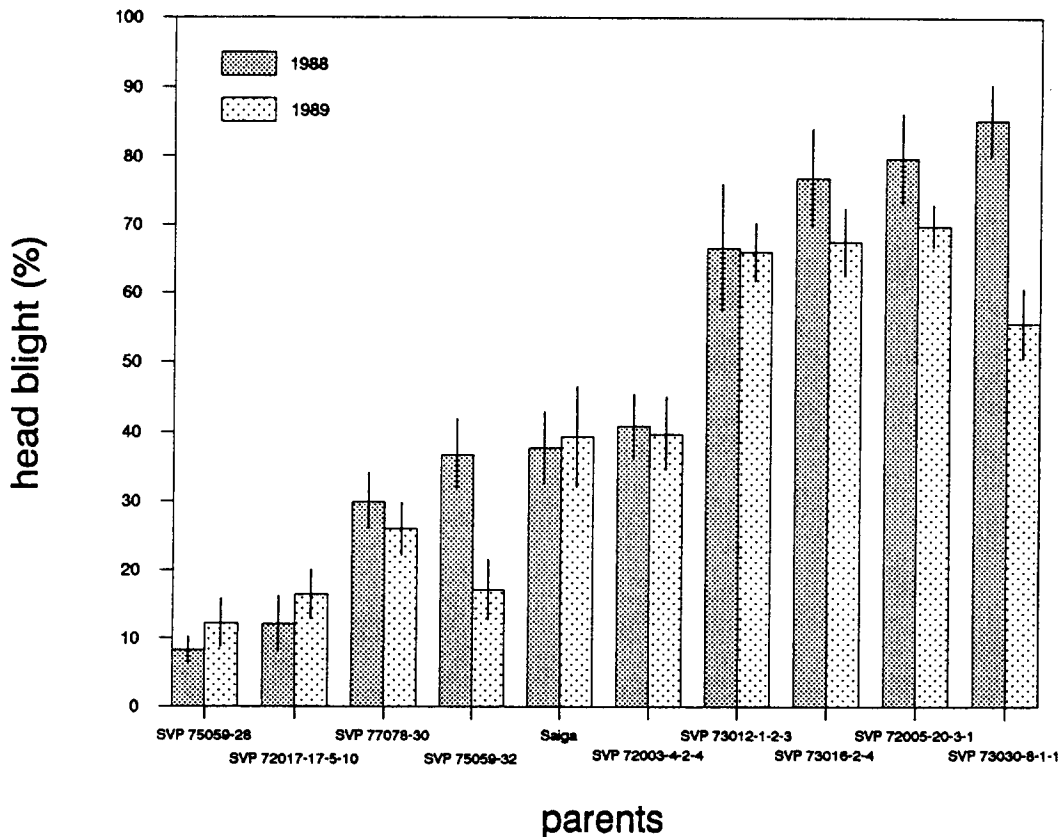
Fig. 1. Levels of resistance to head blight and their confidence interval (P = 0.05) in 10 parental lines after inoculation with *Fusarium culmorum* strain IPO 39-01 in 1988 and in 1989.

two years were closely related (r = 0.93). It may be concluded that genotype × year interaction for Fusarium head blight was small. An exception was parent SVP* 75059-32, which did not react the same as in 1988. Snijders & Van Eeuwijk (1990) concluded that the selections from cross SVP 75059, among them SVP 75059-32, showed a higher genotype × year interaction compared to other genotypes, including all other parents tested in this study. Therefore, one should be cautious with respect to conclusions for offspring of SVP 75059-28 and especially SVP 75059-32. The arithmetic mean head blight incidence of the 10 parental lines was lower in 1989 than in 1988. Therefore, the data of 1988 were corrected by linear regression

* the Foundation for Agricultural Plant Breeding (SVP) is now part of the Centre for Plant Breeding Research (CPO)

with a coefficient of 0.77 and a constant of 4.84 before calculating $\bar{p}$, $\bar{p}'$, S and R.

For six parents, the environmental variance between-plots, σ^2_{eB}, was not significantly different from 0 (P = 0.01). Three of the four parents with a significant σ^2_{eB} in 1989 also showed a significant σ^2_{eB} in 1988. These genotypes apparently show a higher genotype × environment interaction. The high value of the σ^2_{eW} to σ^2_{eB} ratio indicated that the field was homogeneous. The weighted environmental within-plot variance $\bar{\sigma}^2_{eW}$ was 214.9 ± 12.6. This is almost twice the environmental variance estimated for 1988. There was no correlation between mean head blight ratings and variances of the ten parental lines (r = 0.09).

Table 1 presents for each family the following results: the mean head blight ratings of the original F_2 family in 1988 ($\bar{p}$), the mean head blight in 1988 of the sample of selected plants ($\bar{p}'$), the number of

selected plants n($\bar{p}'$), the proportion (%) of selected plants out of the F_2 family, the selection differential S, the mean head blight of the progeny produced by the selected parents based on F_3 line means ($\bar{p}_1$), the number of plants of the total progeny n($\bar{p}_1$), the selection response R, the realized heritability h_r^2 and the number of F_3 lines per cross which showed a transgression for resistance significant at P = 0.05.

Table 1. Mean *Fusarium culmorum* (IPO 39-01) head blight rating (%) of the original 25 winter wheat F_2 families in 1988 ($\bar{p}$)*, the mean head blight rating (%) in 1988 of the selected sample of resistant plants ($\bar{p}'$), the number of selected plants n ($\bar{p}'$), the proportion (%) of selected plants out of the F_2 family, the selection differential S, the mean head blight rating (%) of the progeny produced by the selected plants based on F_3 line means ($\bar{p}_1$), the number of plants of the total progeny n ($\bar{p}_1$), the selection response R, the realized heritability h_r^2 and the number of F_3 lines which showed significant transgression for resistance (P = 0.05). Parental lines are listed in descending order of their resistance in 1988

Cross	Cross number	1988					1989		R	h_r^2	Trans-gression
		$\bar{p}$	$\bar{p}'$	n($\bar{p}'$)	proportion (%)	S	$\bar{p}_1$	n($\bar{p}_1$)			
SVP 75059-28 ×											
SVP 72017-17-5-10	8718	26.3	9.0	16	21.9	17.3	19.3	293	7.0	0.41	2
SVP 77078-30	8735	23.8	9.2	15	23.4	14.5	22.4	322	1.4	0.09	
SVP 75059-32	8728	21.2	4.8	3	33.3	16.4	43.2	43	− 22.0	0.00	
Saiga	8743	24.3	9.4	11	19.0	14.9	22.7	284	1.6	0.11	
SVP 72003-4-2-4	8716	34.4	4.8	1	1.9	29.6	25.0	4	9.4	0.32	
SVP 73016-2-4	8720	38.8	8.7	5	6.3	30.1	34.0	112	4.8	0.16	
SVP 72005-20-3-1	8717	44.3	8.7	1	2.1	35.6	22.6	22	21.7	0.61	
SVP 72017-17-5-10 ×											
SVP 75059-32	8724	25.3	9.2	7	10.0	16.1	22.9	111	2.4	0.15	1
Saiga	8739	23.2	9.5	6	18.2	13.8	27.0	95	− 3.8	0.00	
SVP 72003-4-2-4	8702	36.3	7.7	3	4.8	28.6	29.4	36	6.9	0.24	
SVP 73016-2-4	8709	36.3	8.1	5	8.8	28.2	45.9	123	− 9.6	0.00	
SVP 72005-20-3-1	8703	50.6	4.8	2	2.8	45.8	60.0	11	− 9.4	0.00	
SVP 73030-8-1-1	8713	54.5	4.8	1	1.4	49.6	42.5	4	12.0	0.24	
SVP 77078-30 ×											
SVP 75059-32	8736	34.1	7.4	3	4.1	26.7	26.2	59	7.9	0.29	1
Saiga	8745	34.1	6.4	1	1.5	27.7	19.5	17	14.6	0.53	
SVP 72003-4-2-4	8729	25.2	7.6	10	16.7	17.5	18.7	147	6.5	0.37	5
SVP 73016-2-4	8733	41.6	4.8	1	5.6	36.8	27.5	4	14.1	0.38	
SVP 72005-20-3-1	8730	45.3	6.4	1	1.8	38.9	45.8	26	− 0.5	0.00	
SVP 75059-32 ×											
Saiga	8744	35.1	11.4	2	4.9	23.7	21.2	32	13.9	0.59	1
SVP 72003-4-2-4	8722	26.9	7.7	4	7.3	19.2	34.8	47	− 7.9	0.00	
SVP 73016-2-4	8726	41.1	11.0	2	6.1	30.1	34.0	53	7.1	0.24	
SVP 72005-20-3-1	8723	47.4	6.8	2	3.4	40.7	50.2	10	− 2.8	0.00	
SVP 73030-8-1-1	8727	34.8	7.9	5	6.4	26.9	30.3	53	4.5	0.17	
Saiga ×											
SVP 72003-4-2-4	8737	31.1	9.5	2	4.3	21.6	44.8	25	− 13.7	0.00	
SVP 72003-4-2-4 ×											
SVP 73016-2-4	8707	38.4	10.3	1	4.0	28.1	11.3	8	27.1	0.96	1

* the data of 1988 were corrected by linear regression with a coefficient of 0.77 and a constant of 4.84

Discussion

Selection response

Selection responses averaged 3.7% on the head blight percentage scale and ranged from -22.0% to 27.1%. Realized heritabilities averaged 0.23 and ranged from 0 to 0.96 (Table 1). Negative responses must be explained by the fact that the selected plants obviously had escaped infection in 1988. Where a simple additive-dominance model is adequate, the response to selection (R) is equal to the product of the heritability in narrow sense h_n^2 and the selection differential (S) (Mather & Jinks, 1982). For 17 out of the 25 families from which plants were selected in 1988 the additive-dominance model could be tested on basis of F_1 and F_2: the model satisfied for all 17 families (Snijders, 1990b). However, only estimates for heritabilities in broad sense h_b^2 were obtained from that study. If we compare the realized heritabilities calculated in 1989 (Table 1) with the broad sense heritabilities estimated from the components of variance in 1988 (Snijders, 1990b), in 7 out of 25 families the h_r^2 was higher than the h_b^2. This means that for these families the obtained gain in resistance was higher than expected from the estimates of components of variance in the F_2 generation. However, it should not be overlooked that the estimates of h_b^2 were not very accurate (Snijders, 1990b). The average realized heritability $\overline{h}_r^2$ was 0.23 compared to a $\overline{h}_b^2$ of 0.39.

Transgression

Based on the F_3 line means, six out of 25 crosses showed significant transgressive segregation for a higher resistance (P = 0.05; Table 1). Three resistant F_3 lines showed a resistance higher than that of the most resistant parental line, SVP 75059-28: two F_3 lines from cross 8718, the cross between the most resistant parents, with head blight levels and confidence intervals (P = 0.05) of 4.6% ± 1.5 and 5.9% ± 2.2, respectively, and one F_3 line from cross 8729 with an infection level of 6.7% ± 3.0. In the 1988 trial, for the crosses with a moderately or

highly resistant parent, only in the F_2s of 8718 and 8716 transgressive segregation was clearly observed, and for susceptibility only (Snijders, 1990b). In this study the transgression for resistance found for the F_3 lines gives evidence that the resistance genes in the resistant parents were partly different from one another. This confirms the suggestion in Snijders (1990b) and agrees with their pedigrees which had no ancestors in common (Snijders, 1990a). Accumulation of resistance genes is herewith shown to be possible.

Fixation of resistance genes

Single plant selection in the F_2 proved to be very successful. The speed of selective advance depends on the number of units of inheritance which contribute to the additive genetic variance and the non-additive genetic variance. The greater the proportion of additive heritable variation, the more effective is the selection (Mather & Jinks, 1982). The resistance to Fusarium head blight in the selected populations must be inherited mainly in an additive way, and the number of resistance genes in which the parents differ must be small. If there was mainly additive genetic variance, $\overline{h}_r^2$ should be equal to $\overline{h}_b^2$. The fact that $\overline{h}_r^2$ was lower dan $\overline{h}_b^2$ might be explained by the important number of selected plants which were not resistant but had escaped infection in 1988.

It is obvious that there is a relationship between mean and variance of the F_3 lines (r = 0.56; Fig. 2). Analysis of variance of the head blight data of the parental lines had shown that there was no correlation between mean and environmental variance. In Fig. 2, the dotted line indicates the level of weighted environmental variance $\overline{\sigma}^2_{ew}$. Within the F_3 lines with a high mean head blight resistance, and especially within those F_3 lines which were significantly more resistant than their most resistant parent, genetic variance was small or absent. These lines are probably fixed for Fusarium head blight resistance and will not segregate in later generations. The number of plants of the original F_2 for each family averaged 52, with a maximum of 80 plants. If the parents had differed in three independently
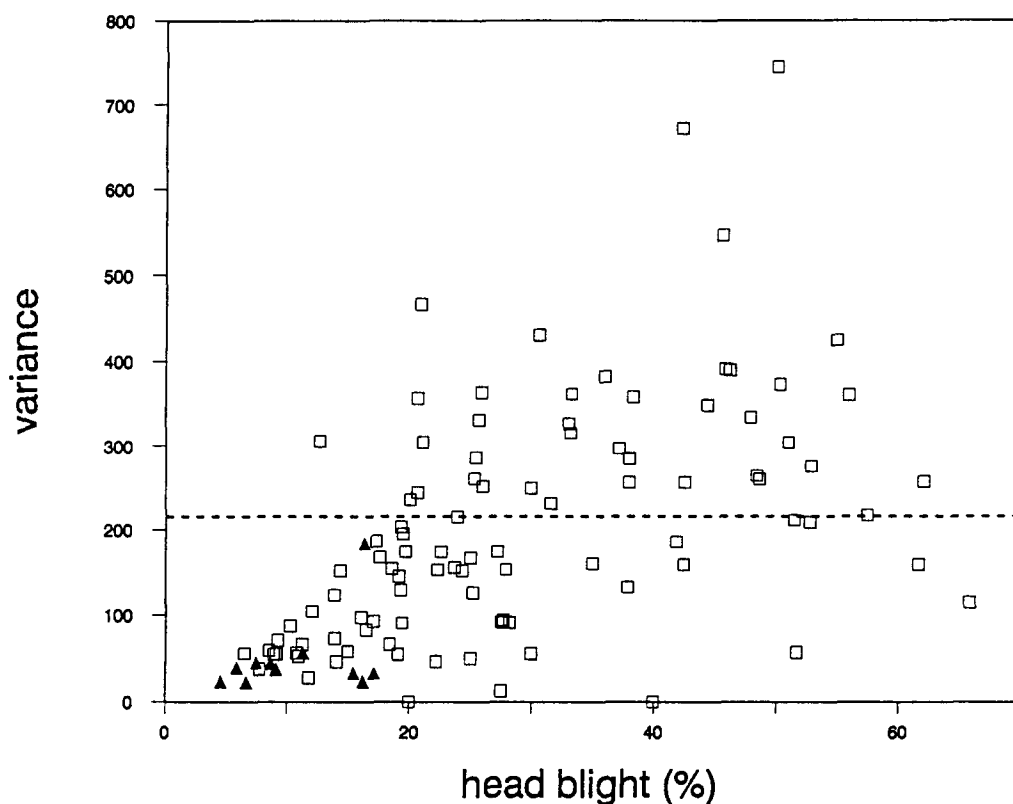
Fig. 2. The relationship between the mean head blight reactions against their variances for all F_3 lines after inoculation with *Fusarium culmorum* strain IPO 39-01 in 1989. The horizontal dotted line indicates the weighted within-plot variance $\bar{\sigma}^2_{ew}$. ▲ indicates F_3 lines with significant transgression (P = 0.05).

segregating resistance genes, in the F_2 only one individual in 64 would have been homozygous for each of the extreme genotypes. Not merely would the chance of immediate fixation under selection be very small, it is even unlikely that any extreme resistant genotype would have been picked up in an F_2 of this size. This would indicate that the parents of which the offspring showed transgression in the F_2 may differ in only one or two resistance genes.

General combining ability

In this study the response to the truncation selection was studied per F_2 family, in order to search among crosses for the better ones, and to concentrate on the elite crosses. The truncation selection over the whole F_2 population resulted in selection of plants from merely those families with one or

two resistant parents (Table 1). Transgression for resistance of F_3 lines was also merely found in these families. In retrospect, it proved superfluous to study the many F_2 families of the 10 × 10 half diallel, as performance of the parent appeared to be a good indicator of the potential of their crosses for resistance breeding. This confirms the conclusion from the combining ability analysis of the 10 × 10 half diallel that specific combining ability effects were unimportant and general performance of the parent was in agreement with its general combining ability (Snijders, 1990a). However, one exception was made for genotype SVP 72003-4-2-4, which had a high general combining ability which was not in accordance with its resistance level. Also, Table 1 shows that crosses with this moderately susceptible genotype resulted in offspring with very high resistance levels and transgression for resistance. Snijders (1990b) suggested that in crosses with SVP

72003-4-2-4 an epistatic gene effect might be present. This could explain the high resistance levels of the offspring. As one F_3 line was even more resistant than the most resistant parent used in this study, and the variance within this line was negligible, epistasis might be of additive × additive gene interaction and fixed in this line.

Early generation selection

An important question in many breeding programs is in which generation selection should take place. Snijders (1990b) concluded that the two resistant parents SVP 75059-28 and SVP 72017-17-5-10 differed from the susceptible parent SVP 72005-20-3-1 in four and five genes, respectively. From this study it was concluded that the two resistant parents differ in one or two genes. This means that the fixed resistance from the selected F_3 lines may differ from a common, susceptible wheat genotype in as much as six genes. In the F_2 of this cross only one in 4^6 plants will contain all resistance genes. Thus, for early selection in the F_2 the population should be very large and the selection pressure lenient. For a practical breeding program, it would be better to delay selection till the F_3 or F_4, where homozygotes have formed an increased proportion of the segregates and the likelyhood for advance under selection will be increased. However, selection will be only successful if there is a uniform and adequate disease pressure in the nursery where the selection takes place.

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