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Assessing non-specificity of resistance in wheat to head blight caused by inoculation with European strains of *Fusarium culmorum*, *F. graminearum* and *F. nivale* using a multiplicative model for interaction

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Abstract To determine whether resistance to Fusarium head blight in winter wheat is horizontal and non-species specific, 25 genotypes from five European countries were tested at six locations across Europe in the years 1990, 1991, and 1992. The five genotypes from each country had to cover the range from resistant to susceptible. The locations involved were Wageningen, Vienna, Rennes, Hohenheim, Oberer Lindenhof, and Szeged. In total, 17 local strains of *Fusarium culmorum*, *F. graminearum*, and *F. nivale* were used for experimental inoculation. One strain, *F. culmorum* IPO 39–01, was used at all locations. Best linear unbiased predictions (BLUPs) for the head blight ratings of the genotypes were formed within each particular location for each combination of year and strain. The BLUPs over all locations were collected in a genotype-by-environment table in which the genotypic dimension consisted of the 25 genotypes, while the environmental dimension was made up of 59 year-by-strain-by-location combinations. A multiplicative model was fitted to the genotype-by-environment interaction in this table. The inverses of the variances of the genotype-by-environment BLUPs were used as weights. Interactions between genotypes and environments were written as sums of products between genotypic scores and environmental scores. After correction for year-by-location influence very little variation in environmental scores could be ascribed to differences between strains. This provided the basis for the conclusion that the resistance to Fusarium head blight in winter wheat was of the horizontal and non-species specific type. There was no indication for any geographical pattern in virulence genes. Any reasonable aggressive strain, a *F. culmorum* strain for the cool climates and a *F. graminearum* strain for the warmer humid areas, should be satisfactory for screening purposes.

Key words Head blight · Resistance breeding
Genotype-by-environment interaction · Multiplicative interaction · Host-specificity

Introduction

Fusarium head blight, a fungal disease of wheat and other small cereals is found in both temperate and semi-tropical regions. A number of species of *Fusarium* may be responsible, but generally *F. graminearum* Schwabe, with perfect stage *Gibberella zeae* (Schw.), and *F. culmorum* (W.G. Smith) Sacc., perfect stage unknown, predominate as the causal factor for *Fusarium* head blight (Lemmens et al. 1993, Mesterhazy 1977, Stack and McMullen 1985, Wilcoxson et al. 1988, Zadoks and Rijswijk 1984). Very exceptionally, *F. avenaceum* (Fr.) Sacc. has been reported to be highly pathogenic (Arseniuk et al. 1993) and *F. nivale* (Fr.) Ces. (Marasas et al. 1984) predominating (Daamen et al. 1991). Species frequencies are influenced by geography, climate and year. *Fusarium graminearum* and *F. culmorum* are non-host specific, i.e. they are pathogenic to wheat, maize and other cereals and grasses without showing specialization for any one crop. Nevertheless, some host prefences among *Fusarium* spp. have been observed

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(Arseniuk et al. 1993). Significant interactions between strains of *F. graminearum* or *F. culmorum* and wheat genotypes have been reported (Mesterhazy 1984, 1988, Snijders and van Eeuwijk 1991). However, the interaction patterns were not stable over experiments and genotype ranking was only slightly influenced by the strains. No evidence has been found for the occurrence of races of *F. culmorum* or *F. graminearum* adapted to different wheat genotypes. To what extent resistance to *F. culmorum* is related to resistance to *F. graminearum* is not clear. Mesterhazy (1983, 1988) found correlation coefficients of up to 0.90 between the reaction of wheat genotypes to *F. culmorum* isolates and their reaction to *F. graminearum* isolates. Spring wheat genotypes which had been reported to be resistant to head blight caused by *F. graminearum* were also resistant to *F. culmorum* (Snijders 1990). Miedaner et al. (1993) concluded for 16 rye inbreds that the genetic basis of resistance to head blight caused by the two *Fusarium* species is very probably the same. Also, Arseniuk et al. (1993) concluded that the cereal resistance to a broad range of *Fusarium* spp. including the above two should be considered at the genus and not at the species level.

In this paper an international study using observations from six locations in five European countries will be presented. This study was initiated to assess the (non-)specificity of head blight resistance in wheat for *Fusarium* spp. and for strains within them, and was coupled to a geographical distribution of virulence genes. The variable selected to represent resistance was visually assessed Fusarium head blight rating. As the data were taken from ongoing research programmes that were not primarily developed towards the question addressed in this paper, the data had a rather complicated structure. Not all locations participated every year, at particular locations different genotypes and strains were used over the years, and experimental design differed between locations. Therefore, special statistical methodology had to be used in which a multiplicative model for the interaction of genotypes with environments (strain-by-location-by-year combinations), that took into account differences in precision, played a central role.

Materials and methods

Years and locations

During the years 1990, 1991 and 1992, 25 wheat genotypes were tested for resistance to Fusarium head blight (FHB). The genotypes were tested at six locations across Europe, namely Wageningen in the Netherlands, Gross-Enzersdorf near Vienna in Austria, Le Rheu near Rennes in France, Hohenheim (350 m altitude) and Oberer Lindenhof (600 m altitude) near Stuttgart in Germany and Szeged in Hungary (Fig. 1).

Genotypes

All genotypes were winter type wheats. From each participating country 5 genotypes covering the range from resistant to susceptible were tested. Variety names, line codes and origins are given in Table 1. The 5 Austrian lines were tested only in 1991 and 1992.

Fig. 1 The six locations and participating countries across Europe at which 25 winter wheat genotypes were tested for Fusarium head blight resistance. Wageningen in The Netherlands, Gross-Enzersdorf near Vienna in Austria, Le Rheu near Rennes in France, Hohenheim and Oberer Lindenhof near Stuttgart in Germany and Szeged in Hungary

Strains

Seventeen local strains of *F. culmorum*, *F. graminearum* and *F. nivale* were used for experimental inoculation (Table 2). The strain *F. culmorum* IPO 39–01 was used at all locations. In Wageningen, each year inoculum production was started up from an ampoule of lyophilized monospored spores. Vienna started up inoculum production from monospores and stored the cultures in earth medium culture (Lemmens et al. 1993). Rennes and Szeged stored the strains on Potato Dextrose Agar (PDA). The strains used in Oberer Lindenhof and Hohenheim were stored in earth medium culture. Wageningen produced inoculum consisting of purely conidiospores on a wheat/oat seed mixture (Snijders and van Eeuwijk 1991). In Rennes, conidiospores of *F. culmorum* were produced on autoclaved, soaked barley. *F. nivale* was produced on PDA at 10°C under near-ultra-violet light. Szeged and Vienna produced an inoculum suspension containing conidiospores and mycelium by continuous aeration of an inoculated liquid Czapek-Dox medium (Mesterhazy 1978). The German locations produced a suspension of conidiospores and mycelium by continuous aeration of an inoculated SNA medium (Nirenberg 1981).

Each participant used its own familiar inoculation method and assessment scale, listed in Table 3. Basically, the inoculation methods applied can be divided into two types. Type 1 method uses the method published by Mesterhazy (1978, 1983). Wheat lines are inoculated at anthesis by spraying 20 ml inoculum suspension containing spores and mycelium on separate bunches of 20–25 heads. Controls are treated with distilled water. The bouquets are then covered with a plastic bag for 24 h. Type 2 method is described by Snijders and van Eeuwijk (1991) and Saur (1991). Whole field plots are inoculated with conidiospores when 30% of the genotypes is flowering. This is repeated two or three times with intervals of 3–4 days until all genotypes are flowering. During the 2 weeks after inoculation a sprinkler irrigation guarantees a high relative humidity.

Table 1 Name, donor, origin, and mean head blight rating of the wheat varieties and lines

Wheat genotype	Donor	Origin	Mean (in %)
SVP 75059-28	CPRO-DLO, Wageningen, the Netherlands	CPRO-DLO	40
Arina	CPRO-DLO, Wageningen, the Netherlands	EFAP Zürich, Switzerland	31
SVP 72005-20-30-1	CPRO-DLO, Wageningen, the Netherlands	CPRO-DLO	67
SVP 72017-17-5-10	CPRO-DLO, Wageningen, the Netherlands	CPRO-DLO	31
SVP 75059-32	CPRO-DLO, Wageningen, the Netherlands	CPRO-DLO	56
NR-172/90	BOKU, Vienna, Austria	Saatzucht Neuhof/Rohrau, Austria	51
P 4371.88	BOKU, Vienna, Austria	Probstdorfer Saatzucht, Austria	64
P 2118.89	BOKU, Vienna, Austria	Probstdorfer Saatzucht, Austria	58
SL 8/80–28	BOKU, Vienna, Austria	Saatbau Linz, Austria	54
SL 34/81–12	BOKU, Vienna, Austria	Saatbau Linz, Austria	51
Copain	INRA, Rennes, France	Ets. C. Benoist, France	44
Rescler	INRA, Rennes, France	INRA	55
RC 103	INRA, Rennes, France	INRA	41
82 F3 28	INRA, Rennes, France	INRA	34
81 F3 79	INRA, Rennes, France	INRA	34
25/83/02	LSA, Hohenheim, Germany	LSA	64
47/83/02	LSA, Hohenheim, Germany	LSA	53
77/82/01	LSA, Hohenheim, Germany	LSA	62
163/81/03	LSA, Hohenheim, Germany	LSA	48
204/81/03	LSA, Hohenheim, Germany	LSA	58
Zombor GKI	CRI, Szeged, Hungary	CRI	65
Szoke GKI	CRI, Szeged, Hungary	CRI	48
Bence GKI	CRI, Szeged, Hungary	CRI	46
85-92 GKI	CRI, Szeged, Hungary	CRI	49
Sgv/GT-Pdj*UhrGK	CRI, Szeged, Hungary	CRI	47

Table 2 Name, species, donor and origin of *Fusarium* strains used in the experiments and presence of the strains at the locations. The code refers to the strain as represented in Fig. 2D

Code	Strain	*Fusarium* spp	Donor	Isolated from	Presence at location					
					Wageningen	Vienna	Rennes	Hohenheim	Ob Lindenhof	Szeged
1	IPO 39–01	*F. culmorum*	Wageningen	bread wheat (Flevina) kernel	+	+	+	+	+	+
2	SVP 8901	*F. culmorum*	Wageningen	bread wheat (Kanzler) head	+					
3	SVP 8904	*F. culmorum*	Wageningen	bread wheat (Beatrix) head	+					
4	91031	*F. graminearum*	Vienna	durum wheat kernel		+				
5	91047	*F. graminearum*	Vienna	durum wheat kernel		+				
6	91015	*F. culmorum*	Vienna	durum wheat kernel		+				
7	Le Rheu 89–4	*F. culmorum*	Rennes	bread wheat kernel			+			+
8	Le Rheu mix	*F. culmorum*	Rennes	bread wheat kernel			+			
9	F. nivale Fn002	*F. nivale*	Rennes	durum wheat (Durelle) kernel			+			
10	HOH 200/207 mix	*F. graminearum*	Hohenheim	bread wheat/durum wheat kernel				+	+	
11	HOH 214/223 mix	*F. culmorum*	Hohenheim	durum wheat head				+	+	
12	F.g. 12216	*F. graminearum*	Szeged	bread wheat kernel (6947/7)						+
13	F.g. 13377	*F. graminearum*	Szeged	maize crown						+
14	F.c. 12375	*F. culmorum*	Szeged	wheat crown						+
15	F.c. 12551	*F. culmorum*	Szeged	wheat lower stem						+
16	F.c. D 223	*F. culmorum*	Szeged (strain from Hoh.)	durum wheat head						+
17	F.g. D 207	*F. graminearum*	Szeged (strain from Hoh.)	durum wheat kernel						+

Data

Head blight symptoms were observed on different scales (Table 3). For analysis all Fusarium head blight (FHB) ratings were first expressed on a 0–100 scale of which subsequently the logit (=log(FHB/(100-FHB))) was taken. At Wageningen, in addition to the FHB rating, yield and thousand kernel weight reduction were measured as described in Snijders (1990). Also flowering date was observed. In Vienna the extra measurement concerned yield reduction and ear weight reduction based on ten heads. In Rennes, the extra measurements besides the FHB rating consisted of yield and thousand kernel weight loss, determined by comparison with the control: in 1990 and 1991, on a whole hill plot basis (Saur and Trottet 1992); in 1992, on basis of a sample of 40 heads. Also, the percentage damaged (pink) kernels was assessed based on a sample of 500 seeds. At the German locations, besides the FHB rating, yield components were determined based on ten heads and expressed as a percentage of the non-infected control (Mesterhazy 1978, 1983). In Szeged, the

Table 3 Inoculation method and Fusarium head blight (FHB) assessment scale used at each testing location

Location	Inoculation method	FHB-scale[a]	Observation after
Wageningen	type 2/field plots	0–100%	28 days
Vienna	type 1/bunch of heads	0.0–4.0	22 days
Rennes	type 2/field plots	1.0–9.0	450°days in 1990 350°days in '91/'92
Hohenheim	type 1/bunch of heads	1–9	31 days
Oberer Lindenhof	type 1/bunch of heads	1–9	22 days
Szeged	type 1/bunch of heads	0.0–4.0	18, 22, 26 and 30 days For analysis the means were used

[a] Lowest value indicates no symptoms; highest value indicates 100% infection

extra measurement concerned yield reduction based on ten heads (Mesterhazy 1978, 1983) and percentage grain infection estimated as percentage white/pink kernels.

FHB was chosen as the variable whose analysis had to elucidate the type of resistance. The factors whose effect had to be quantified before being able to answer that question were genotype, year, location and strain. FHB data were unbalanced with respect to these four factors taken together. The 5 Austrian genotypes were absent in all the trials of 1990. Also in 1990, the Austrian strains 91015, 91031 and 91047, and the French *F. nivale* were not used at any location. In 1991, strain 91015 was again absent, in this case together with the Le Rheu mix from France, the latter also being absent in 1992. Year-by-location combinations that were not available, were Vienna in 1990 and Oberer Lindenhof in 1992. For the presence of strain-by-location combinations, see Table 2.

General strategy of analysis

The general methodology chosen to answer the question on the type of resistance is an extension of an approach developed earlier towards the same problem in Snijders and van Eeuwijk (1991). Resistance will be defined as horizontal if no genotype-by-strain interactions can be found over years and locations. Firstly, analyses per location were done to determine whether genotype-by-strain interactions were stable over years within the individual locations. Mixed models, models with fixed and random terms (Searle 1971), were fitted per location. Parameters were estimated by residual maximum likelihood (Patterson and Thompson 1971) using Genstat (1993). Interest focussed on the genotype-by-strain interaction and the genotype-by-strain-by-year interaction. The presence of a genotype-by-strain interaction in combination with the absence of a genotype-by-strain-by-year interaction should indicate resistance of the strain-specific type.

For each location, genotype-by-environment two-way tables of best linear unbiased predictions, or BLUPs (Robinson 1991, Verdooren 1992), were calculated based on the fitted mixed model. The environments in these tables consisted of the combinations of strains and years present at a particular location. For some environments no BLUPs were available for the 5 Austrian genotypes. The genotype by environment tables per location were then combined over all six locations to give a 25-(genotypes) by-59 (environments=location-by-year-by-strain combinations; see Table 4) two-way table that served as the basis for the overall analysis. For the answer to our research question on the type of resistance only the interaction in this table was relevant. Let x_{ij} be the residual from additivity for the i-th genotype in the j-th environment, which is what is left of the BLUP after correction for the main effects of genotype and environment. The residual from additivity, x_{ij}, can be separated in structure and noise. One way to do that is by means of a singular value decomposition of the matrix of residuals from additivity. The singular value decomposition of the matrix with the entries x_{ij} writes each x_{ij} as the sum of a number of product terms:

$$x_{ij} = c_{1i} \times d_{1j} + c_{2i} \times d_{2j} + \ldots + c_{Ki} \times d_{Kj},$$

where c_{1i} to c_{Ki} represent the genotypic scores for genotype i, and d_{1j} to d_{Kj} the corresponding environmental scores for environment j. In principle, K is equal to the minimum of I-1 and J-1, with I the number of rows and J the number of columns. That is, for a 25×59 table, 24 product terms can be estimated. However, usually the first few product terms suffice for an adequate description of the interaction structure. The rest of the product terms are then collected in a residual representing noise. The residual from additivity is thus decomposed as

$$x_{ij} = c_{1i} \times d_{1j} + c_{2i} \times d_{2j} + \ldots + c_{Ni} \times d_{Nj} + e_{ij},$$

where the product terms express the structure, e_{ij} the noise, and N the number of products necessary for adequate description. Application of this method to complete two-way tables is rather straightforward (Gabriel 1978, Gauch 1988, Snijders and van Eeuwijk 1991). Because the Austrian genotypes were not present in 18 of the 59 environments and because it was deemed better to weigh the BLUPs by the inverse of their variances, an adapted method was used to estimate main effects and product terms simultaneously, taking into account incompleteness of the table and differential weighting of the entries (Denis 1991, van Eeuwijk 1995). Product terms that were retained as structure were those whose relative contribution to the interaction sum of squares exceeded the average per term of 4.2% (100% divided by 24, the latter number giving the number of product terms available for a table of 25 by 59; Jolliffe 1986).

For determining the type of resistance, only the environmental scores are of importance. If for the environmental scores the effect of years, locations, or their joint (interaction) effect dominates the effect of strains, this is an indication for non-specificity of the resistance. To be sure, also the joint (interaction) effect of strains and years, strains and locations, and strains, years and locations must be considered and proven negligible. The assessment of the effect of the different environmental factors on the environmental scores can take place in several ways. Very informally, one can plot the environmental scores (Kempton 1984), d_{2j} against d_{1j} to start with, and inspect the resulting plot on clustering of environments due to shared strains or other factors. If the environments cluster mainly on the basis of strains this is a strong argument for the existence of strain specific resistances. More formally, one can perform an analysis of variance on the environmental scores, treat d_{1j} to d_{Nj} as individual variables, and assess the importance of the strains after correction for years and locations. Finally, one can look at the environmental scores d_{1j} to d_{Nj} simultaneously, again interpreting them as variables, and carry out two discriminant analyses on them: firstly, using strains as a grouping factor and secondly, using year-by-location combinations. The 'variables' d_{1j} to d_{Nj} are used to construct discriminant functions. The number of discriminant functions that can be formed is equal to the minimum of the number of groups in the grouping factor minus 1 and the number of variables. These discriminant functions are linear combinations of the original variables, e.g. the first discriminant function can be calculated as $b_{11}d_{1j} + b_{12}d_{2j} + \ldots + b_{1N}d_{Nj}$. The weights b_{pq} for the q-th variable in the p-th discriminant function are chosen so that the between-groups variation is maximized with respect to the within variation. Roughly said, this means that the first discriminant function is that linear combination of the original variables that has the highest F value possible in an analysis of variance on basis of the grouping factor used for construction of the discriminant function. The second discriminant function is the linear combination giving the second highest F value under the re-

Table 4 Environmental means for head blight rating in percent. Code A and B refer to the location-year-strain combinations as represented in Fig. 2A and B

Plot code		Environment	Mean
A	B		
1	1	Wageningen 1990 IPO39-01	18
2	1	Wageningen 1990 SVP8901	4
3	1	Wageningen 1990 SVP8904	13
4	2	Wageningen 1991 IPO39-01	54
5	2	Wageningen 1991 SVP8901	22
6	2	Wageningen 1991 SVP8904	24
7	3	Wageningen 1992 IPO39-01	79
8	3	Wageningen 1992 SVP8901	13
9	3	Wageningen 1992 SVP8904	16
10	4	Vienna 1991 IPO39-01	86
11	4	Vienna 1991 91031	64
12	4	Vienna 1991 91047	89
13	5	Vienna 1992 IPO39-01	77
14	5	Vienna 1992 91015	48
15	5	Vienna 1992 91031	56
16	5	Vienna 1992 91047	66
17	6	LeRheu 1991 IPO39-01	68
18	6	LeRheu 1991 LeRheu 89–4	57
19	7	LeRheu 1992 IPO39-01	83
20	7	LeRheu 1992 LeRheu 89–4	68
21	8	LeRheu 1990 LeRheu mix	80
22	6	LeRheu 1991 F.nivale	51
23	7	LeRheu 1992 F.nivale	60
24	9	Hohenheim 1990 HOH 200/207 mix	71
25	9	Hohenheim 1990 HOH 214/223 mix	88
26	10	Hohenheim 1991 IPO39-01	97
27	10	Hohenheim 1991 HOH 200/207 mix	94
28	10	Hohenheim 1991 HOH 214/223 mix	96
29	11	Hohenheim 1992 IPO39-01	89
30	11	Hohenheim 1992 HOH 200/207 mix	79
31	11	Hohenheim 1992 HOH 214/223 mix	87
32	12	Oberer Lindenhof 1990 HOH 200/207 mix	58
33	12	Oberer Lindenhof 1990 HOH 214/223 mix	74
34	13	Oberer Lindenhof 1991 IPO 39-01	94
35	13	Oberer Lindenhof 1991 HOH 200/207 mix	82
36	13	Oberer Lindenhof 1991 HOH 214/223 mix	94
37	14	Szeged 1990 LeRheu 89-4	62
38	14	Szeged 1990 F.g.216	11
39	14	Szeged 1990 F.g.377	61
40	14	Szeged 1990 F.c.375	50
41	14	Szeged 1990 F.c.551	52
42	14	Szeged 1990 F.c. D 223	61
43	14	Szeged 1990 F.g. D 207	49
44	15	Szeged 1991 IPO39-01	51
45	15	Szeged 1991 LeRheu 89-4	31
46	15	Szeged 1991 F.g.216	17
47	15	Szeged 1991 F.g.377	16
48	15	Szeged 1991 F.c.375	46
49	15	Szeged 1991 F.c.551	24
50	15	Szeged 1991 F.c. D 223	20
51	15	Szeged 1991 F.g. D 207	43
52	16	Szeged 1992 IPO39-0101	4
53	16	Szeged 1992 LeRheu 89-4	5
54	16	Szeged 1992 F.g.216	3
55	16	Szeged 1992 F.g.377	24
56	16	Szeged 1992 F.c.375	43
57	16	Szeged 1992 F.c.551	10
58	16	Szeged 1992 F.c. D 223	6
59	16	Szeged 1992 F.g. D 207	4

striction that it is orthogonal to the first discriminant function, etc. After calculation, discriminant functions can be treated as ordinary variables. A mean for every group of environments can be calculated. Then one can check each of the environments for the group mean it is closest to and allocate the environment to that group. This is what we call the a posteriori classification. The original grouping is called the a priori classification. The principle does not change when we consider classification on more than one discriminant function. Large differences between group membership in a priori and a posteriori classifications shows that the grouping used for a priori classification does not make much sense with respect to the variation found in the variables used for construction of the discriminant functions. So, if the a priori classification according to strains differs considerably from the a posteriori classification there is not much reason to assume strain specificity of the resistance. An extra argument for that conclusion would be close correspondence between a priori and a posteriori classification on year-by-location basis.

Designs and analyses per location

Experimental design differed between locations and sometimes between strains per location. As mentioned above, mixed models were fitted to the data collected for a particular location or for the data collected for a particular location by strain combination, as for Rennes.

Wageningen

In each of the 3 years a split plot design was used with three replicates (blocks), strains as main plots and genotypes as sub plots (2.00×0.75 m) (Snijders and Van Eeuwijk 1991). The nine combinations of location, year and strain involved correspond to the environments 1–9 in Table 4. A mixed model was fitted to the complete set of data collected in Wageningen; that is, a model was fitted for all of the genotypes over the environments 1–9. BLUPs were calculated for each of the environments, i.e. for environments 1, 2 and 3 for 20 genotypes (Austrian genotypes absent in 1990), for environments 4–9 for all 25 genotypes. In the mixed model used the fixed terms were g + s + y + gs + gy + sy and the random terms gsy + yb + ybs + ybsg, where g stands for genotype, s for strain, y for year and b for block. Letters alone represent main effects, their combinations interactions.

Vienna

Vienna participated in 1991 and 1992, with 3 and 4 strains, respectively, thus defining the environments 10–16 in Table 4. In both years the wheat genotypes were sown in 10 m^2 plots. Each genotypic plot was then split in three parts or repeats (r). Within each repeat plants of the particular genotype were inoculated with every one of the strains to be evaluated in that year. Fixed terms for the analysis of environments 10–16 were g + s + y + gs + gy + sy, random terms gsy + ygr + ygrs.

Rennes

Evaluations from the environments 17–20 of Table 4 were analysed together. The combinations involved were the years 1991 and 1992 and the *F. culmorum* strains IPO 39–01 and Le Rheu 89–4. Within each year the strains were evaluated independently of each other on hill plots (20 seeds, 50 cm apart) in a randomized complete-block design with three replicates. That is, each block contained all of the genotypes within the particular *F. culmorum* strain. The model used for analysis was: fixed terms g + s + y + gs + gy + sy; random terms gsy + ysb.

In 1990 there were also evaluations of all genotypes except the Austrian ones inoculated by a Le Rheu mix. This is environment 21 in Table 4. The evaluations took place in a randomized complete blocks design with six replicates. The model fitted was simple: fixed g; random bg. (Random components with negative estimates for the

corresponding variance component were removed from models. In this case b was removed.)

Rennes was the only location where *F. nivale* was used for inoculation. In 1991 and 1992, environments 22 and 23 in Table 4, randomized complete-block designs were used in two and three replicates, respectively. The model included the fixed terms g + y + gy, and the random terms gyb.

Hohenheim

The design was comparable to that used in Vienna, except that field plots were 7.5 m^2, and two repeats were used within each genotype. The model used to analyse environments 24–31 of Table 4 was the same as to that used for Vienna.

Oberer Lindenhof

This was a location in 1990 and 1991. The design and model were the same as those of Hohenheim. The environments are 32–36 in Table 4.

Szeged

The design was the same as that of Vienna. Field plots were 5 m^2. Plots were subdivided in three repeats (Mesterhazy 1988). The model contained for the fixed terms g + s + y + gs + gy + sy + gsy and random term ygrs. The environments in question were 37–59 in Table 4.

Results

Table 5 shows that in general FHB ratings were highly correlated with yield reduction and weight reduction. Anthesis dates in Wageningen showed that flowering time did not influence infection levels.

The most important result from the analyses of the FHB ratings per location was that within each location significant genotype-by-strain-by-year interaction was present. (For Rennes, of course, no three way interaction could be determined for the evaluations with the Le Rheu mix and *F. nivale*.) Consequently, no straightforward determination of the type of resistance as strain specific or vertical seemed possible. However, the environmental scores per location on average were clustered more by year than by strain (not shown). This finding did not support an interpretation of the resistance as vertical. Because the pattern of the environmental scores that emerged from the overall analysis over the six locations was almost a superposition of the six analyses per location, the patterns per location will not be dealt with individually.

The overall analysis on the two-way table of BLUPs indexed by the 25 genotypes on one side and the 59 environments on the other side showed that the environmental main effect accounted for 81.9% of the variation in the table and the genotypic main effect for 5.0%. Tables 1 and 4 contain the genotypic and environmental means, after back transformation to percentages. One should be cautious with the interpretation of differences between the genotypic means, as the non-additivity, comprising 13.1% of the total variation, is considerable, and in fact precludes unconditional interpretation. For the structural part of the non-additivity five product terms, -together accounting for 77.8% of that non-additivity-, were judged to be relevant. These five product terms exceeded the critical value of 4.2%, and accounted for respectively 44.1, 11.5, 9.0, 6.7, and 6.5% of the interaction sum of squares.

Table 5 Pearson correlation coefficients based on means over replicates per location between Fusarium head blight infection level (FHB), yield reduction, weight reduction and visible kernel infection

	Yield reduction	Weight reduction	Kernel infection
FHB			
Wageningen	0.82	0.84	–
Vienna	0.77	0.73	–
Rennes *F. culmorum* 1990/1991	0.03	0.30	0.08
Rennes *F. culmorum* 1992	0.86	0.62	0.44
Rennes *F. nivale* 1991	–	0.71	–
Rennes *F. nivale* 1992	0.47	0.29	–
Hohenheim	0.51	0.79	–
Oberer Lindenhof	0.58	0.83	–
Szeged	0.78	–	0.71
kernel infection			
Rennes *F. culmorum* 1990/1991	0.91	0.80	
Rennes *F. culmorum* 1992	0.61	0.52	
Szeged	0.71	–	

In Fig. 2A–D the environmental scores corresponding to the two most explaining product terms are plotted. Fig. 2A just gives an overview of the 59 environments from Table 4. To facilitate closer inspection different plotting symbols are used: in Fig. 2B, year-by-location (Table 4), in Fig. 2C, *Fusarium* species, and in Fig. 2D, strains. Figure 2B shows that environments belonging to the same year-by-location combination tend to cluster; Fig. 2C illustrates that *Fusarium* species cannot be distinguished by their position; and Fig. 2D illustrates that environments cannot be distinguished on the basis of the strains. Special attention must be given to strain 1, IPO 39–01, which was used at all locations. The points for IPO 39–01 are scattered all over the plot. If there had been a case for strain specific resistance, the points for IPO 39–01 should have been close together. Therefore, Fig. 2 shows that year-by-location effects dominate *Fusarium* species and strain effects in the interaction with the genotypes, and supports the hypothesis of non-species specificity of the resistance. The plot for the two most explaining product terms may be seen as characteristic for all other possible plots that could have been made, like the third against the first term, the third against the second, etc. All plots more-or-less revealed the same pattern, that of dominating year-by-location effects.

More formally, this was also found in the analyses of variance on the environmental scores of the product terms one to five. First the amount of variation in the environmental scores of a particular term due to differences in year-by-location groups was calculated. Next, the amount of variation due to strains after correction for year-by-location effects was calculated. What was then left, represented variation due to the interaction between year-by-location effects and strains. For environmental scores corresponding to the first product term 85.7% was due to year-by-location effects, 6.7 to strain effects after correction for year-

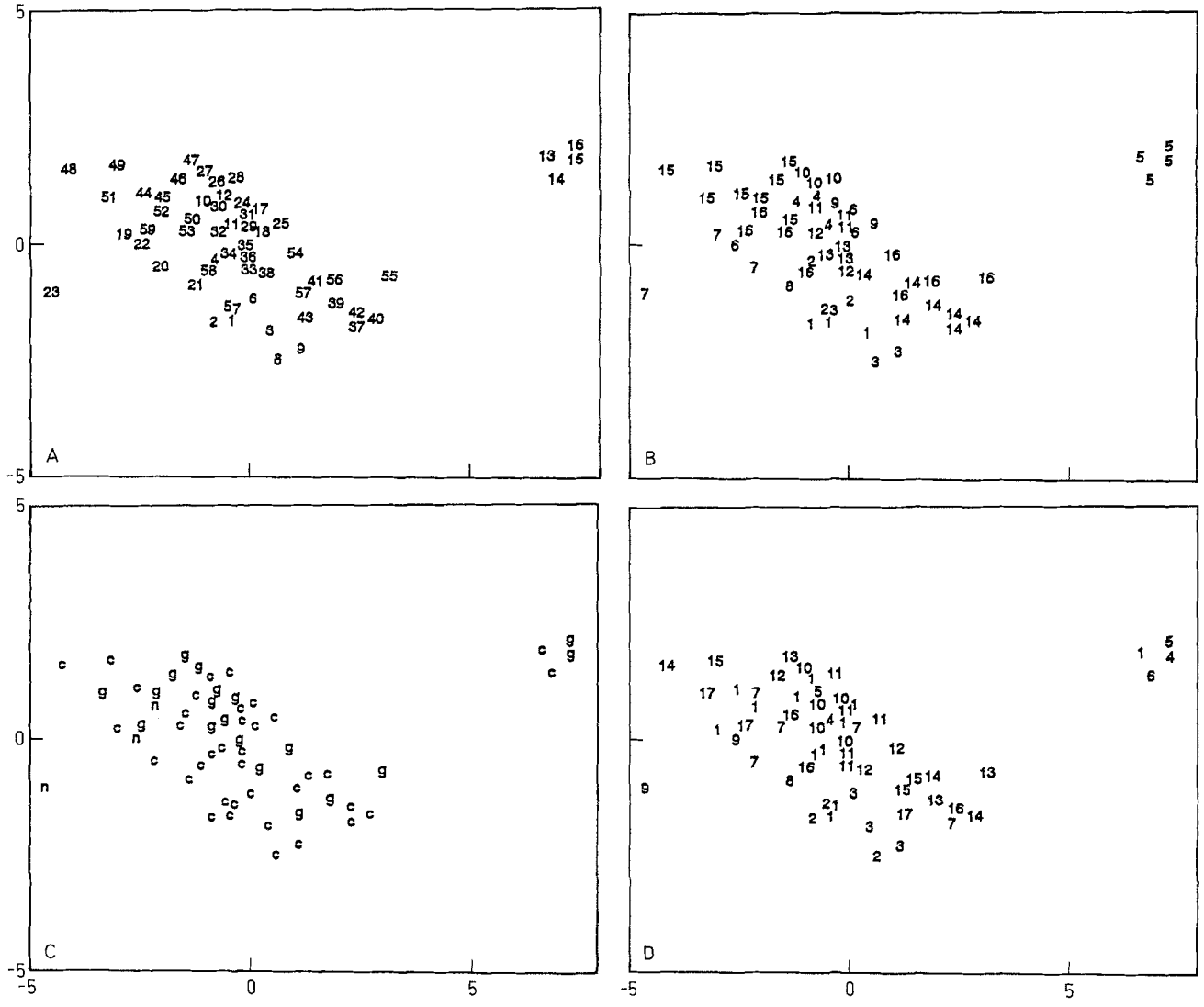

Fig. 2 Plots of environmental scores indexed by **A** environmental codes of Table 4, **B** year by location codes of Table 4, **C** *Fusarium* species (*c culmorum, g graminearum, n nivale*), **D** strain numbers of Table 2

by-location effects, and then 7.6% was left for the interaction between both grouping factors. The same quantities for environmental scores of the second product term were; 89.9, 4.8, and 5.2; for the third; 77.2, 9.4, and 13.4; for the fourth; 77.1, 12.4 and 10.5; and for the fifth; 72.1, 9.8 and 18.1. It is clear that after correction for year by location effects, strain effects contribute very little to the variation in environmental scores. Interaction between genotypes and environments can be described to a major extent as interaction between genotypes and the environmental circumstances due to the combination of year and location. Consequently, there seems no reason to assume species specific resistance.

A last argument for that thesis is provided by the discriminant analyses using either a year-by-location grouping factor or a strain grouping factor and using as variables the environmental scores belonging to the first five product terms of the interaction. For the year by location case only 6 out of the 59 environments were not allocated to the year by location group they came from. In contrast, using the strains as grouping factor only 19 environments were correctly allocated; 40 were wrongly allocated. This once again shows the strong prevalence of year-by-location effects over strain effects.

Discussion

Inoculation method

The data do not allow a firm conclusion to be made about which of both inoculation methods is preferable. Still, a major interaction occurred in Vienna in 1992 due to a change in the weather during inoculation. An extremely hot and dry period with low infection pressure was succeeded by a humid and cool period with higher infection pressure. However, even for these extreme environmental circumstances no differentiation between the strains could be observed with respect to their interaction with the wheat

genotypes. Within all locations the same dominance of year-by-location effects occurred, irrespective of the inoculation method used. Nevertheless, it is recommended to avoid unnecessary interactions of whichever type. The inoculation method giving rise to the smallest interactions should therefore be used.

FHB rating as selection criterion

The size of the correlations of FHB with yield reduction and percentage *Fusarium*-infected kernels showed that the FHB rating is a reliable selection criterion for resistance. This was concluded earlier by Mesterhazy (1990), Snijders (1990), and Miedaner et al. (1993).

Specificity of FHB resistance

There seems to be no reason for believing that the resistance to Fusarium head blight as caused by *F. culmorum* is specific. The same is true for *F. graminearum*. Neither is there any indication for a geographical pattern in virulence genes. Furthermore, the resistance to *F. graminearum* and *F. nivale* seems to be of the same type as that to *F. culmorum*. Any reasonable aggressive strain, a *F. culmorum* strain for the cool climates, a *F. graminearum* strain for the warmer humid areas, should be satisfactory for screening purposes. This confirms the results of Snijders and van Eeuwijk (1991) for *F. culmorum* strains from The Netherlands and the results of Mesterhazy (1983, 1988) for Hungary. Shuttle programmes for selection for *Fusarium* head blight resistance are unnecessary.

The dependence of aggressiveness of strains on the environmental circumstances, which to a large extent are unpredictable, complicates the choice of strain. Screening programmes can be safeguarded by the inclusion of a number of strains, whether pure isolates or mixtures, having varying sensitivities to the environment (Lemmens et al. 1993, Mesterhazy (1984, 1987), Snijders and van Eeuwijk 1991).

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