Genetic Variation for Virulence and Resistance in the Wheat-*Mycosphaerella graminicola* Pathosystem II. Analysis of Interactions Between Pathogen Isolates and Host Cultivars

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ABSTRACT

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Nonparametric and parametric statistical procedures were employed to analyze six data sets, comprising 80 pathogen isolates and 47 host cultivars, to investigate the presence and relevance of interaction in the wheat-*Mycosphaerella graminicola* pathosystem. Each data set was confined to either responses of bread wheat to bread wheat-derived isolates or of durum wheat to durum wheat-derived isolates, and to each of two disease parameters, presence of necrosis (*N*) and production of pycnidia (*P*). Four data sets were employed for explorative statistical analyses that involved a procedure using the size of the overall variances for cultivars and isolates in tables of effects to estimate the relative proportions of specific factors for resistance and virulence in host and pathogen genotypes, respectively. Subsets, comprising cultivars and isolates with either high or low variances, were selected from the data matrices and subjected to analyses of covariance. Subsets that included entries with high variances revealed interaction mean squares that explained approximately 25% of the total variance, which was considerably higher than in the complete data matrices. The results indicated considerable genetic variation for specific resistance and virulence factors in host and pathogen, respectively, and, therefore, for the effectiveness of the procedure. Analysis of subsets that were confined to entries with low variances resulted in interaction mean squares that contributed little to the total variance, which was an indication of the absence of differential responses, that might be because of either susceptible or resistant responses to all applied pathogen isolates. Two data sets were obtained by an additional experiment, involving 15 *M. graminicola* isolates and 24 host cultivars in two replications, that was conducted to design a selection experiment to test hypotheses that were based on preceding statistical analyses. This experiment, which involved small subsets of isolates and cultivars, confirmed the hypothesis that a large overall variance may be indicative of specific factors for virulence or resistance. It also indicated that a low overall variance was not necessarily indicative of nonspecific resistance. In all cases, parametric and nonparametric statistical procedures showed significant interactions between pathogen isolates and host cultivars. Similar results were obtained for both disease parameters, although differences between these parameters were evident. The employed statistical procedures and the additional data demonstrated specificity in the relationship between either bread wheat or durum wheat and *M. graminicola*. This suggested a gene-for-gene relationship in these pathosystems that requires further elucidation and may have important repercussions on breeding strategies.

Additional keywords: durability, pathogenic variation, rank-interaction, *Septoria tritici*, *Triticum aestivum*, *Triticum turgidum* subsp. *durum*.

An ideal gene-for-gene relationship in plant-pathogen interactions requires a locus in the host that governs either a resistant or a susceptible response, and a locus in the pathogen that governs either a virulent or an avirulent response (24). This relationship has often been described using the 'quadratic check' involving two host cultivars and two pathogen isolates that differ in only one gene for resistance and virulence, respectively. These 'ideal' gene-for-gene relationships are usually confined to pathosystems that involve organisms with genes that confer major effects, which results in distinct well-defined qualitative disease classes (e.g., the cereal rusts). Pathosystems involving host and pathogen genotypes with less pronounced qualitative characteristics are generally studied using quantitative approaches, such as analysis of variance. Gene-for-gene relationships are often suggested by significant statistical interactions between pathogen and host genotypes, but usually without providing unequivocal evidence for specificity in such a pathosystem (8,9,25,26). Thompson and Burdon (29) listed over 40 associations between plants and pathogens that were either demonstrated or suggested to have such an interaction. These examples mostly involved biotrophic pathogens, but also included necrotrophic and hemibiotrophic pathogens. Others, such as *Mycosphaerella graminicola* (Fuckel) J. Schröt. in Cohn (anamorph: *Septoria tritici* Roberge in Desmaz.), *Stagonospora nodorum*, and *Pyrenophora tritici-repentis* were not referred to, though a gene-for-gene relationship was also suggested to apply to these pathogens, albeit primarily based on

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statistical evidence for interaction (9,25,26). Genetic variation for virulence in *M. graminicola*, an important fungal pathogen of bread wheat and durum wheat (*Triticum aestivum* L. and *T. turgidum* L. (Thell.) subsp. *durum* L., respectively), has been debated since Eyal et al. (7) suggested physiologic specialization in it. However, the perception of a gene-for-gene relationship in the wheat-*M. graminicola* pathosystem remained controversial. This is primarily because of i) the suggestion that specificity for wheat species dominates the specificity for particular cultivars of those species, ii) the deficiency of examples of cultivars that quickly succumbed to new strains of the pathogen, and iii) the small proportions of the total variance in analyses of variance that were explained by interaction (8,9,15,32). In addition, Van Ginkel and Scharen (31) performed a diallel analysis and found general combining ability (GCA) to be the major component of variation, though specific combining ability (SCA) effects were also significant. A generation mean analysis also indicated the importance of additive gene effects (30). They, therefore, suggested that their results could indicate the absence of gene-for-gene relationships, implying genetic variation for aggressiveness rather than for virulence among *M. graminicola* isolates (31,32).

Leonard (18) reviewed research on northern leaf blight of maize caused by *Setosphaeria turcica*. In this pathosystem, it was also demonstrated that GCA and SCA effects were significant, though GCA effects were much larger than SCA effects and a generation mean analysis indicated that additive gene action was of major importance. Nevertheless, there was also evidence for specificity, though field populations did not provoke a detectable decline of quantitative resistance. In this pathosystem, and in the relation between *Cochliobolus heterostrophus* and maize, there was conclusive evidence of adaptation by the pathogen to (partially) overcome polygenic resistance in maize (18). However, the genetic differentiation among *C. heterostrophus* strains was not always apparent from the interaction mean squares (MS_{int}) in analyses of variance, which were therefore not considered to be entirely appropriate to demonstrate specificity in a pathosystem. Significance of host × pathogen interactions may depend on experimental design, actual proportions of genes with general and specific effects (10,12,18,19), or experimental conditions (6,11). Moreover, Vanderplank (33) pointed out that parametric analyses, including analysis of variance, are sensitive to the way disease is assessed, a problem which is circumvented by the application of nonparametric procedures.

Kema et al. (17) discussed genetic variation for virulence and resistance in the wheat-*M. graminicola* pathosystem, and considered two disease parameters, i.e., the presence of necrosis and pycnidia. Highly significant MS_{int} values for each of these parameters were determined in analyses of covariance (ANCOVAs) that involved separate analyses of data sets from either bread wheat or durum wheat and *M. graminicola* isolates originating from these species.

In the present study, parametric and nonparametric statistical analyses were employed to i) test for specificity in the wheat-*M. graminicola* pathosystem, and ii) select cultivars and isolates with presumed specific factors for resistance and virulence, respectively, in order to investigate the reproducibility of observed interactions between such cultivars and isolates.

TABLE 1. Experimental code and origin of 15 *Mycosphaerella graminicola* isolates that were studied for genetic variation for virulence toward 23 wheat cultivars and one triticale cultivar

ECI[y]	Isolate	Country	Location
MX1	*IPO*90001	Mexico	Toluca
MX2	*IPO*90002	Mexico	Toluca
MX3	*IPO*90003	Mexico	Toluca
MX4	*IPO*90004	Mexico	Patzcuaro
MX5	*IPO*90005	Mexico	Juchitepec
MX6[z]	*IPO*90006	Mexico	Toluca
MX7	*IPO*90007	Mexico	Toluca
MX8	*IPO*90008	Mexico	Juchitepec
MX9	*IPO*90009	Mexico	Juchitepec
MX10	*IPO*90010	Mexico	Juchitepec
MX11	*IPO*90011	Mexico	Juchitepec
MX12[z]	*IPO*90012	Mexico	Patzcuaro
EC1	*IPO*90013	Ecuador	Alausi
PU1	*IPO*90014	Peru	Andenes
PU2[z]	*IPO*90015	Peru	Andenes

[y] ECI = experimental codes for isolates.
[z] Isolates selected for specificity tests.

TABLE 2. Nonparametric analysis for two-way layouts, involving response matrices for the bread wheat-*Mycosphaerella graminicola* pathosystem (48 isolates and 19 cultivars), and the durum wheat-*Mycosphaerella graminicola* pathosystem (11 isolates and 18 cultivars), and the disease parameters *N* (necrosis) and *P* (pycnidia) estimated as percentages on primary wheat leaves, averaged over pots (Kema et al. [17])

Pathosystem	T[u]	df[v]	T_1[w]	df	T_2[x]	df
Bread wheat						
N	1,839[y]	864	15[z]	18	1,824[y]	846
P	1,908[y]	864	13[z]	18	1,895[y]	846
Durum wheat						
N	253[y]	187	10[z]	17	243[y]	170
P	425[y]	187	5[z]	17	420[y]	170

[u] T = Kruskal-Wallis statistic, for differences between cultivars and cumulative for the number of blocks (i.e., isolates) involved.
[v] df = degrees of freedom, calculated as $I(C-1)$ for T, $C-1$ for T_1, and $(C-1)(I-1)$ for T_2, in which I is the number of isolates and C is the number of cultivars involved.
[w] T_1 = Friedman statistic, for differences between blocks (i.e., isolates).
[x] T_2 = statistic for rank interaction.
[y] Highly significant, $P < 0.01$, χ^2_{df} approximation.
[z] Not significant, because of the correction for cultivar main effects.

MATERIALS AND METHODS

Nonparametric and explorative parametric statistical analyses. Four data sets, that were adjusted for block (i.e., time effects) (17), were available for further statistical analyses. They comprised 19 bread wheat cultivars and 48 bread wheat-derived isolates and 18 durum wheat cultivars and 11 durum wheat-derived isolates. The two disease parameters, *N* for necrosis and *P* for pycnidia, estimated as percentages on the primary leaves, respectively (17), were studied individually.

The nonparametric method involved a procedure for two-way layouts, according to De Kroon and Van der Laan (4). These authors introduced a concept of rank-interaction between the classifying factors of a two-way table with equal numbers of observations per cell, and a concomitant distribution-free test for significance. Essentially, the procedure involves a combination of the Kruskal-Wallis and Friedman nonparametric tests. For large samples, the test statistics of both tests were approximately chi-square distributed. Kruskal-Wallis test statistics were separately calculated for differences between cultivars (treatments) by assigning rank numbers to the samples within each isolate (block), and were subsequently cumulated over blocks. The Friedman statistic for differences between cultivars was calculated for the complete table, classified by isolates and cultivars. The cumulated Kruskal-Wallis statistic T was decomposed into two components, T_1 and $T_2 = T - T_1$, in which T_1 was the aforementioned Friedman statistic. Under the H_0 hypothesis of no interaction between isolates and cultivars, the test statistics T_1 and T_2 were approximately independent and distributed according to a chi-square distribution. Statistic T_1 accounted for differences between cultivars, whereas T_2 was sensitive to differences in ranking orders of host cultivars within isolates. A suggested procedure to correct for main effects by calculating the sample medians for each row and

column to calibrate the data was adopted (4), and the equality of the ranking orders of the host cultivars for the *M. graminicola* isolates was tested.

The explorative statistical procedure involved parametric analyses as proposed by Eberhart and Russell (5). They employed regression analysis for estimating stability parameters to compare cultivars over different environments, which was adapted by Leonard and Moll (19) for host-pathogen systems. The model was further advanced by Jenns et al. (12) and later simplified by Jenns and Leonard (10). The procedure was of particular interest, since it provided estimates for relative specificity in pathosystems involving quantitative aspects of resistance and/or virulence, and was, therefore, considered to be appropriate for a further evaluation of specificity in the wheat-*M. graminicola* pathosystem (17). Hence, the data sets were subjected to ANCOVAs and a table of effects was generated for each data set, which comprised only interaction components for each host-isolate combination, i.e., actual disease severities minus main effects for cultivars and isolates. This table of effects was used to calculate overall variances for both disease parameters (σ^2_N and σ^2_P) for each isolate and cultivar to estimate the relative specificity for virulence and resistance in pathogen and host genotypes, respectively (10).

ANCOVAs on subsets of isolates and cultivars were employed to study the effects of matrix size and selection on the proportion of the MS_{int} in the total variance.

Additional experiments. To substantiate the evidence for specificity in the wheat-*M. graminicola* pathosystem and to evaluate the aforementioned suggested statistical procedures empirically, two additional experiments were conducted. The first experiment involved inoculations of a tester set of 24 accessions that was similar to the one employed in previous experiments (17), with 15 monopycnidial *M. graminicola* isolates that were obtained according to procedures described earlier (16) and stored over silica gel at –20 and –80°C before use (Table 1). The second experiment was conducted after selection of cultivars and isolates with high σ^2_P values and comprised four bread wheat cultivars and three bread wheat-adapted *M. graminicola* isolates, and two durum wheat cultivars and two durum wheat-adapted *M. graminicola* isolates.

Experimental design and data analyses. The first experiment was carried out according to a split-plot design with two replications and was analyzed by analysis of variance. The experimental procedures and conditions were similar to those described earlier (17). The data enabled the selection of isolates and cultivars, which were suggested to carry a relatively large fraction of specific factors (high σ^2_P values). Four years later, these isolates and cultivars were again tested in a split-plot verification experiment with two replications over time. An interaction between two durum wheat cultivars and two durum wheat-adapted *M. graminicola* isolates was retested in the same experiment. The statistical analysis of the verification experiment differed from the analyses of the large previous experiments (17), since the degrees of freedom for the residual variance were coherent with the size of experiments. Transformation of the data in large experiments (17) did not substantially stabilize the residual variance and did not influence the conclusions. In small experiments, however, stabilization of the residual variance was appropriate. The verification experiment was, therefore, analyzed using a generalized linear model (GLM) with logit link and variance function proportional to $M(100 - M)$, in which M is the mean disease parameter.

RESULTS

Nonparametric statistical analyses of bread wheat and durum wheat data sets. The distribution-free procedure for two-way layouts showed the presence of rank-interactions, since the T_2 test statistics were significant at $P < 0.01$ (Table 2). Exposing cultivars to different *M. graminicola* isolates in both systems, and for both response parameters, resulted in significant ranking differences. The nonsignificance of the T_1 statistic was because of the correction for main effects (Table 2).

Parametric statistical analyses of bread wheat and durum wheat data sets. Calculation of σ^2_P for each cultivar involved and subsequent ranking from low to high provided, together with the overall means, a useful estimator of relative specificity of the resistance in these cultivars (Tables 3 and 4). A high σ^2_P level is always an indication for fluctuating responses toward *M. graminicola* isolates, therefore, possibly for a relatively large proportion of specific resistance factors. Low σ^2_P levels, however, suggest either a relatively large proportion of general resistance factors or a relatively small proportion of such factors, i.e., no or unmatched specific resistance. Cultivars such as 'Veranopolis' and 'Kavkaz/7C' had among the highest σ^2_P, but low overall P

TABLE 3. Estimates for relative specificity of resistance in 19 bread wheat cultivars to 48 *Mycosphaerella graminicola* isolates, quantified and ordered by the size of the calculated overall variance for the disease parameters P (pycnidia) and N (necrosis), σ^2_P and σ^2_N, respectively, for each cultivar in the tables of effects[x]

Cultivar	ECC[y]	σ^2_P	$P_{overall}$[z]	σ^2_N	$N_{overall}$[z]
Iassul 20	Ia	49	5	160	46
Beth Lehem	BL	52	6	78	38
Kavkaz/K4500 l.6.a.4	KK	74	5	229	25
Bobwhite	Bo	79	8	101	25
Ceeon	Ce	90	34	133	51
Kavkaz	KZ	95	10	480	48
Arminda	Ar	96	6	411	38
Kavkaz/UP 301	KU	103	11	210	28
Colotana	Co	105	11	112	50
Lakhish	La	115	37	109	57
Shafir	Sh	118	40	112	63
Toropi	To	153	18	206	62
Taichung 29	T29	162	32	75	77
Gerek 79	Ge	172	41	190	73
Olaf	Ol	181	28	232	50
Obelisk	Ob	182	24	163	58
Veranopolis	Ve	202	13	505	32
Klein Titan	KT	222	42	146	76
Kavkaz/7C	K7	225	17	412	44

[x] Figures are based on four replicates over time (Kema et al. [17]).
[y] ECC = experimental codes for cultivars.
[z] Mean over 48 *M. graminicola* isolates, in four replications, for each cultivar.

TABLE 4. Estimates for relative specificity of resistance in 18 durum wheat cultivars to 11 *Mycosphaerella graminicola* isolates, quantified by calculation of the overall variance for the disease parameters P (pycnidia) and N (necrosis), σ^2_P and σ^2_N, respectively, for each cultivar in the tables of effects[x]

Cultivar	ECC[y]	σ^2_P	$P_{overall}$[z]	σ^2_N	$N_{overall}$[z]
Jori	Jo	36	56	47	66
Triticum dicoccoides G25	G25	57	12	96	55
Safir	Sa	70	51	111	64
Inrat 69	I69	80	29	116	79
Inbar	In	86	69	77	73
M. B. Bachir	MB	117	53	93	72
Cocorit	Cc	124	53	71	75
Acsad 65	A65	127	49	159	60
Hedba 3	H3	132	57	156	82
BD 2777	BD	140	33	133	81
Zenati Bouteille	ZB	160	47	114	85
Marzak	Ma	167	59	82	80
OZ 368	OZ	218	38	102	73
Tensift	Te	243	61	41	81
Zenati Bouteille/*T. polonicum*	ZP	276	46	45	75
Bidi 17	B17	287	40	122	68
Waha	Wa	368	46	94	63
Omrabi 5	OR	418	46	109	57

[x] Figures are based on four replicates over time (Kema et al. [17]).
[y] ECC = experimental codes for cultivars.
[z] Mean over 11 *M. graminicola* isolates, in four replications, for each cultivar.

TABLE 5. Estimates for relative specificity of virulence in 48 *Mycosphaerella graminicola* isolates to 19 bread wheat cultivars, quantified by calculation of the total variance for the disease parameters *P* (pycnidia) and *N* (necrosis), σ^2_P and σ^2_N, respectively, for each isolate in the tables of effects[y]

Isolate	σ^2_P	$P_{overall}$[z]	σ^2_N	$N_{overall}$[z]
*IPO*87018	39	17	100	46
*IPO*88027	43	12	146	34
*IPO*88014	44	16	51	57
*IPO*87000	45	13	127	55
*IPO*87008	51	16	110	48
*IPO*88024	55	15	169	57
*IPO*88010	57	28	91	61
*IPO*88021	60	20	193	62
*IPO*87013	61	16	105	52
*IPO*87011	69	25	101	58
*IPO*86063	71	18	216	49
*IPO*86026	73	20	103	58
*IPO*86078	74	15	333	44
*IPO*86010	78	24	107	52
*IPO*88023	80	22	87	49
*IPO*87015	81	19	121	45
*IPO*87012	81	15	199	50
*IPO*87021	89	23	275	45
*IPO*88018	101	24	196	48
*IPO*235	105	7	320	44
*IPO*88005	109	25	123	66
*IPO*88019	111	23	176	58
*IPO*86013	111	29	143	51
*IPO*87009	114	20	132	47
*IPO*87020	123	15	196	50
*IPO*88020	125	22	103	46
*IPO*89012	131	6	258	35
*IPO*88025	131	6	318	42
*IPO*88038	131	21	145	53
*IPO*89010	133	16	286	59
*IPO*87019	139	16	290	41
*IPO*86008	145	22	289	41
*IPO*86023	150	23	209	42
*IPO*87016	150	24	173	42
*IPO*86068	160	33	128	56
*IPO*87024	169	23	342	60
*IPO*88037	169	25	314	54
*IPO*88013	176	13	271	33
*IPO*87023	179	29	298	45
*IPO*88015	180	27	161	51
*IPO*88016	199	32	183	55
*IPO*86009	227	26	209	51
*IPO*88004	238	22	418	50
*IPO*89013	243	8	776	31
*IPO*87022	272	26	481	45
*IPO*89011	327	30	296	57
*IPO*88017	356	21	403	49
*IPO*88022	402	24	346	46

[y] Figures are based on four replicates over time (Kema et al. [17]).
[z] Mean over 19 bread wheat cultivars, in four replications, for each isolate.

TABLE 6. Estimates for relative specificity of virulence in 11 *Mycosphaerella graminicola* isolates to 18 durum wheat cultivars, quantified by calculation of the total variance for the disease parameters *P* (pycnidia) and *N* (necrosis), σ^2_P and σ^2_N, respectively, for each isolate in the tables of effects[y]

Isolate	σ^2_P	$P_{overall}$[z]	σ^2_N	$N_{overall}$[z]
*IPO*91020	46	52	129	77
*IPO*91011	60	53	37	80
*IPO*91016	79	56	81	78
*IPO*91018	94	52	36	66
*IPO*91017	117	53	115	83
*IPO*91015	146	37	141	58
*IPO*91012	176	43	66	76
*IPO*91009	203	47	41	78
*IPO*91004	245	52	115	70
*IPO*91014	263	46	18	70
*IPO*86022	399	25	260	52

[y] Figures are based on four replicates over time (Kema et al. [17]).
[z] Mean over 18 durum wheat cultivars, in four replications, for each isolate.

levels, and were, therefore, considered highly differential in their response to *M. graminicola*, whereas cultivars like 'Iassul 20', 'Beth Lehem', 'Kavkaz/K4500 l.6.a.4', and 'Bobwhite' responded more or less similarly to most of the isolates (low *P* and low σ^2_P). Similar inferences held for the durum wheats and wild emmer accession *T. dicoccoides* 'G25' (Table 4). 'G25', having a low σ^2_P, could carry a large proportion of factors for general resistance or unmatched specific resistance factors compared to 'Omrabi 5', whereas cultivars such as 'Jori', with a low σ^2_P and a high overall *P*, were expected to carry small proportions of general resistance factors and effective specific resistance factors.

Evidently, considerations for *N* and *P* were not congruent, as exemplified by the bread wheat cultivars Arminda and Kavkaz, which had among the highest σ^2_N values, suggesting a relatively large proportion of specific resistance factors, whereas the σ^2_P values directed more towards a relatively small proportion of such factors (Table 3). In contrast, the durum wheat cultivars had almost invariably high *N* levels, thus, relatively low σ^2_N values were expected (Table 4).

An analogous procedure for the *M. graminicola* isolates provided estimations for the relative proportion of specific virulence factors in these isolates (Tables 5 and 6). The σ^2_P for bread wheat- and durum wheat-derived isolates ranged from about 40 to 400. Isolate *IPO*89013 had a high σ^2_P but a low overall *P*; hence, it carried specific virulence for only a few cultivars. Other isolates with comparable magnitudes of σ^2_P showed a much higher overall *P* level, and could, therefore, carry a larger number of specific virulence factors. Again, comparisons between σ^2_P and σ^2_N were largely contrasting and lead to contradictory hypotheses for the proportions of specific and general virulence factors.

To investigate the effect of matrix size and selection on the proportion of the MS_{int} in the total variance, several ANCOVAs were conducted on restricted data sets. Random restriction of the data matrices, for both *N* and *P*, resulted in larger proportions of the MS_{int}, which suggested that the size of a data matrix irrespective of the genotypes involved influenced the proportion of the MS_{int} (data not shown). Selected small subsets for *N* and *P* that comprised either five bread wheat, or durum wheat, cultivars and five isolates from these species with either the highest or the low-

TABLE 7. Analyses of covariance of the disease parameter *P* (pycnidia) on four data subsets, including five host and pathogen genotypes, which were confined to either bread or durum wheat, and *Mycosphaerella graminicola* isolates which were adapted to these host species[u]

	Bread wheat system		Durum wheat system	
Source of variation	df	MS[v]	df	MS
High σ^2_P levels				
Isolates	4	2,342	4	1,269[w]
Covariates	13	471	9	257
Mainplot error	1	16	6	75
Cultivars	4	2,072	4	4,241
Cultivars × isolates	16	1,760[w]	16	1,991[x]
Subplot error	55(1)	95	60	119
Low σ^2_P levels				
Isolates	4	17	4	169
Covariates	13	35	9	670
Mainplot error	1	22	6	200
Cultivars	4	2,105	4	9,705
Cultivars × isolates	16	39[y]	16	166[z]
Subplot error	69(1)	37	60	133

[u] Each subset included entries with either high or low σ^2_P levels, suggesting a relatively large and small proportion of specific factors for resistance and virulence, respectively.
[v] MS = mean square.
[w] 26% of the total variance.
[x] 25% of the total variance.
[y] 1% of the total variance.
[z] 2% of the total variance.

est σ^2_P levels (Tables 3 and 4) were analyzed as described by Kema et al. (17). The subsets that included cultivars and isolates with high σ^2_P levels resulted in MS_{int} proportions of over 25%, whereas analysis of subsets that included cultivars and isolates with low σ^2_P levels determined MS_{int} proportions of approximately 1% (Table 7). Similar results were obtained for *N* (data not shown). Since significance tests could not be performed because of the a posteriori approach of this analysis, additional experiments were performed.

Parametric and nonparametric statistical analyses of two additional experiments. The responses of the durum wheat and triticale cultivars in the first additional experiment were not included in the tables (Tables 8 and 9), since the *M. graminicola* isolates were adapted to bread wheat, particularly for *P*, which substantiated the evidence for a bread wheat and a durum wheat variant in *M. graminicola* (17).

Cluster analyses, similar to those described by Kema et al. (17), grouped the 15 *M. graminicola* isolates (Table 1) in four and three significantly different clusters for *P* and *N*, and the cultivars in five and three significantly different clusters for *P* and *N*, respectively (data not shown). Hence, cultivars or isolates that were clustered for *N* did not necessarily constitute a similar cluster for *P* and vice versa, which suggested that both parameters were under different genetic control, as was suggested previously (17). For *P*, the isolates were largely separated by location, except for the isolates from Toluca and the two isolates from Peru. Isolates *IPO*90001-MX1, *IPO*90006-MX6, and *IPO*90007-MX7 from Toluca were separated from the others because of the combined virulence for 'Olaf' and 'Kavkaz' and its derivatives. The other isolates from Toluca (*IPO*90002-MX2 and *IPO*90003-MX3) were virulent on 'Olaf' but not on 'Kavkaz' and its derivatives, whereas the reverse was observed for the isolates from Patzcuaro (*IPO*90004-MX4 and *IPO*90012-MX12).

Analyses of variance and the nonparametric procedure of De Kroon and Van der Laan (4) indicated significant cultivar × isolate interactions (Tables 10 and 11). In order to enable the selection of isolates and cultivars with supposedly high proportions of specific virulence and resistance factors, respectively, the data were analyzed according to the aforementioned procedure (10), and the isolates and cultivars were arranged according to the size

TABLE 8. Necrosis (*N*) response matrix of 19 bread wheat accessions to 15 *Mycosphaerella graminicola* isolates[x]

	Cultivars[z]																		
ECI[y]	Bo	KT	Ob	BL	Ia	La	Sh	T29	Co	To	Ce	Ge	KK	Ar	KU	Ol	Ve	K7	KZ	σ^2_N
MX11	18	72	55	25	48	34	48	77	41	40	21	37	3	29	3	21	9	10	18	151
PU1	7	53	35	8	53	33	13	55	11	61	20	28	6	11	5	21	53	3	3	172
MX5	20	82	73	40	92	76	66	78	39	66	49	58	8	58	34	72	37	39	20	185
MX9	19	83	49	9	69	55	39	72	31	45	5	26	5	41	13	46	25	10	13	193
MX10	20	94	81	44	96	46	80	99	40	51	30	57	18	31	30	60	44	39	28	196
MX3	9	81	39	16	56	50	37	88	53	65	51	75	4	5	5	60	30	12	9	201
MX2	34	91	61	27	72	73	49	100	65	79	80	90	15	14	25	86	50	49	24	229
EC1	19	93	53	14	85	56	61	90	54	92	59	95	4	28	23	73	52	26	20	233
PU2	4	60	39	5	50	63	43	85	24	74	56	53	3	28	6	48	66	3	8	304
MX8	5	73	69	23	69	57	49	99	19	43	46	82	7	53	5	52	68	10	8	369
MX7	36	75	75	21	87	63	61	98	72	93	54	87	32	10	82	82	25	97	92	405
MX1	42	94	75	40	73	69	61	92	74	93	29	44	72	22	76	53	34	95	87	434
MX6	30	91	61	41	66	87	55	88	44	73	41	75	73	30	82	66	8	100	82	469
MX12	38	66	45	28	69	28	31	53	27	58	19	79	33	6	3	7	9	10	85	498
MX4	41	93	90	35	93	66	50	88	54	81	68	99	74	51	81	5	42	99	96	552
σ^2_N	89	101	106	118	131	142	154	156	157	168	302	359	381	396	441	584	597	740	778	

[x] Values are means of two replicates. Isolates and cultivars are arranged according to the size of their variance (σ^2_N) in the tables of effects. $LSD_{0.01} = 53$, $LSD_{0.05} = 40$.
[y] ECI = experimental codes for isolates.
[z] Experimental codes for cultivars.

TABLE 9. Pycnidia (*P*) response matrix of 19 bread wheat accessions to 15 *Mycosphaerella graminicola* isolates[x]

	Cultivars[z]																		
ECI[y]	BL	Co	Bo	KK	KT	To	Sh	Ar	Ia	La	Ce	Ge	Ob	T29	KU	Ol	KZ	Ve	K7	σ^2_P
MX8	2	1	1	0	30	2	32	9	7	20	25	34	40	56	0	29	0	0	5	45
MX11	0	3	3	0	19	2	40	1	4	9	9	15	39	47	0	7	1	0	0	69
MX5	9	11	9	2	29	16	51	20	18	49	33	41	43	70	6	48	3	3	7	87
MX3	2	4	0	0	26	19	41	0	0	31	40	44	24	74	0	39	0	12	0	91
MX10	3	4	7	5	38	8	41	11	9	29	19	24	62	71	8	32	0	2	9	95
EC1	0	2	12	0	36	25	52	3	5	16	33	45	17	72	4	44	1	5	7	103
MX9	1	7	7	0	29	7	45	2	12	49	3	11	34	49	0	39	0	0	5	111
MX7	2	20	31	13	26	31	43	0	1	28	42	56	41	64	43	50	41	0	38	128
PU1	0	0	0	0	4	7	8	1	1	18	15	5	8	30	0	6	0	20	0	143
PU2	0	1	0	0	30	19	37	0	5	25	37	32	17	58	0	28	0	43	0	148
MX12	1	1	18	3	25	27	30	0	0	14	12	49	33	40	25	0	32	0	40	171
MX2	3	28	20	2	45	48	32	1	3	55	57	60	42	73	4	59	0	1	24	201
MX6	19	13	21	30	56	40	61	4	1	67	33	53	45	73	49	46	58	0	63	211
MX4	3	4	10	13	17	19	42	8	3	39	42	49	59	25	20	0	15	0	45	212
MX1	16	24	29	36	54	35	53	1	3	52	23	30	47	65	55	33	58	5	66	265
σ^2_P	28	35	35	47	65	68	82	105	111	147	161	167	173	181	186	243	266	274	303	

[x] Values are means of two replicates. Isolates and cultivars are arranged according to the size of their variance (σ^2_P) in the tables of effects. $LSD_{0.01} = 32$, $LSD_{0.05} = 24$.
[y] ECI = experimental codes for isolates.
[z] Experimental codes for cultivars.

of the calculated variances (σ^2_N and σ^2_P, Tables 8 and 9). Hence, isolates and cultivars with assumed specific factors for virulence and resistance, respectively, appeared in the right-bottom part of the tables. Selection of an appropriate subset of cultivars and isolates for the second additional experiment, therefore, considered that section of these tables. Cultivars Olaf, Veranopolis, and Kavkaz were selected and supplemented by 'Kavkaz/K4500 l.6.a.4' for a specificity test. The selected isolates *IPO*90015-PU2, *IPO*90012-MX12, and *IPO*90006-MX6 seemed to carry specific virulence factors for resistance factors in several of these cultivars, including 'Kavkaz/K4500 l.6.a.4' (Tables 8 and 9). Isolates *IPO*86022-TK5 and *IPO*91014-TN6 and cultivars Waha and Hedba 3 were selected to retest an interaction that was observed in a previous experiment (17) between these durum wheat cultivars and durum wheat-adapted *M. graminicola* isolates.

The results of this second additional experiment (Table 12) confirmed previous data (Table 9; and Table 6 in 17) with regard to specificity and demonstrated once more the interactions between host cultivars and pathogen isolates in both pathosystems. For the bread wheat isolates, the *P* level of some cultivars was considerably higher than in the first additional experiment, but did not influence the conclusions on interaction. The cultivar × isolate component of the accumulated analysis of deviance for *N* (data not shown) and *P* was highly significant for both pathosystems (Table 13).

TABLE 10. Analyses of variance of the disease parameters *N* (necrosis) and *P* (pycnidia) of response matrices[v] that comprised 19 bread wheat cultivars and 15 *Mycosphaerella graminicola* isolates, originating from Mexico, Peru, and Ecuador

	N		*P*	
Source of variation	df	MS[w]	df	MS
Isolates	14	6,920[x]	14	2,974[y]
Mainplot error	14	2,363	14	75
Cultivars	18	10,738[y]	18	7,052[y]
Cultivars × isolates	252	656[y,z]	252	297[y,z]
Subplot error	270	316	270	130

[v] Tables 8 and 9, respectively.
[w] MS = mean square.
[x] *F* values significant at $P < 0.05$.
[y] *F* values significant at $P < 0.01$.
[z] The percentage of the total variance for both *N* and *P* is 3.

TABLE 11. Nonparametric analysis for two-way layouts, involving the disease parameters *N* (necrosis) and *P* (pycnidia) of response matrices[s] that comprised 19 bread wheat cultivars and 15 *Mycosphaerella graminicola* isolates, originating from Mexico, Peru, and Ecuador

Disease parameter	T[t]	df[u]	T_1[v]	df	T_2[w]	df
N	311[x]	270	7[z]	18	304[x]	252
P	346[y]	270	7[z]	18	339[y]	252

[s] Tables 8 and 9, respectively.
[t] Kruskal-Wallis statistic, for differences between cultivars, cumulative for the number of blocks (i.e., isolates) involved.
[u] df = degrees of freedom, calculated as $I(C-1)$ for T, $C-1$ for T_1, and $(C-1)(I-1)$ for T_2, in which I is the number of isolates and C the number of cultivars involved.
[v] Friedman statistic, for differences between blocks (i.e., isolates).
[w] Statistic for rank interaction.
[x] Significant at $P < 0.05$, χ^2_{df} approximation.
[y] Highly significant, $P < 0.01$, χ^2_{df} approximation.
[z] Not significant.

TABLE 12. Pycnidia (*P*) response matrix of four bread wheat accessions to three bread wheat-adapted *Mycosphaerella graminicola* isolates and of two durum wheat cultivars to two durum wheat-adapted *Mycosphaerella graminicola* isolates

	Bread wheat cultivars[y]				Durum wheat cultivars[y]	
Isolates	KK	KZ	Ve	Ol	Wa	H3
*IPO*90006 (MX6)	46 a[z]	60 a	5 b	70 a		
*IPO*90012(MX12)	46 a	69 a	8 b	4 b		
PU2	5 b	6 b	66 a	70 a		
*IPO*91014 (TN6)					13 d	57 c
*IPO*86022 (TK5)					51 c	7 d

[y] Experimental codes for cultivars.
[z] Values are backtransformed means of data analyzed on logit scale from two experiments (bread wheat cultivars vs bread wheat-derived isolates, and durum wheat cultivars vs durum wheat-derived isolates) that were conducted over time and comprised two and three replications, respectively. Pairwise comparisons in each experiment were performed between all cells by approximate *t* tests on the transformed scale. Significant differences ($P < 0.01$) are indicated by different letters (a and b; c and d).

DISCUSSION

Statistical interaction is regularly suggested to be an indicator for specificity of virulence and resistance in host-pathogen systems (8,9,25,26). However, lack of statistical interaction does not necessarily support the absence of specificity, since interaction effects might be so small that they will not be detected (23) or might be dependent on environmental conditions (6,11,34). Essentially, the biological implication of statistical evidence for interaction would be strengthened by providing unequivocal examples of interactions between certain host and pathogen genotypes (17). In addition, nonparametric statistics for interaction would strengthen hypotheses of gene-for-gene relationships between such genotypes, since such analyses avoid problems of stretch, i.e., nonhomogeneity of the error.

In the present study of the bread and durum wheat pathosystems, the ranking of cultivars differed significantly between isolates for both response parameters, which corroborated previous data and suggestions for specificity in these pathosystems. Additional analyses involved ANCOVAs of subsets that contained selected wheat cultivars and *M. graminicola* isolates with either low or high σ^2_P values, that were, according to a theoretical model system (10), considered to carry relatively small and large proportions of specific factors, respectively. Analysis of data sets that included host and pathogen genotypes that were considered to carry relatively small proportions of specific factors revealed only a small proportion of the total variance that was explained by interaction, which was of similar size as those described to be significant in other reports (9,14,23,26). The large proportion of the total variance that was explained by interaction in the data set with high σ^2_P values is not inevitable, since high σ^2_P levels do not provide any insight in the genetic structure of the entries. Two entries may have had high σ^2_P values and a similar genetic background; hence, the variance would be explained by main effects. Whenever the interaction component explained a significant proportion of the total variance, different specific resistance and

TABLE 13. Accumulated analyses of deviance of the disease parameter *P* (pycnidia) in two verification experiments[x] that comprised four bread wheat cultivars and three bread wheat-adapted *Mycosphaerella graminicola* isolates and two durum wheat cultivars and two durum wheat-adapted *Mycosphaerella graminicola* isolates, respectively

	Bread wheat system		Durum wheat system	
Change	df	Mean deviance	df	Mean deviance
Blocks	1	113[y]	2	33[z]
Cultivars	3	28[z]	1	0[z]
Isolates	2	17[z]	1	6[z]
Cultivars × isolates	6	150[y]	1	317[y]
Error	11	8	6	8

[x] Table 12.
[y] *F* values significant at $P < 0.01$.
[z] *F* values not significant.

virulence factors may be hypothesized. Therefore, the results supported the hypotheses that the genotypes involved carried different specific factors for resistance and virulence, and that the proportion of the MS_{int} depended on matrix size and on unknown proportions of specific factors in the genotypes involved, which was in accordance with previous data and theoretical models (10,17,23). In addition, these hypotheses were also strengthened in two additional experiments that substantiated the evidence for specificity in the wheat-*M. graminicola* pathosystem. It was an actualization of Ellingboe's (6) statement that nonspecific resistance should be interpreted as resistance that has not yet shown to be specific. Resolving specificity, therefore, seemed to depend on many factors, among which optimal experimental conditions may be of prime importance (8,11,17,34).

Jenns and Leonard's procedure (10) to order host and pathogen genotypes according to σ^2_P, which is suggested to be correlated with the proportion of operational specific factors, pointed to cultivars with high σ^2_P values that might be employed as 'differentials' to elucidate the virulence structure in *M. graminicola* populations. However, cultivars with a low σ^2_P and a low overall *P* level do not necessarily carry relatively large proportions of factors for general resistance, and, thus, could not be classified as potentially durable. Even when dealing with a pathosystem involving typically quantitative aspects of resistance and virulence, such a prediction would be misleading. This warning was illustrated by the virulence for the resistance in 'Kavkaz/K4500 l.6.a.4', which was found in isolates *IPO*90006-MX6 and *IPO*90012-MX12. The broad resistance to *M. graminicola* in this cultivar might be because of just one resistance factor for which virulence in the pathogen population was rare. Studies on the genetics of resistance in wheat to *M. graminicola* indicate that monogenic, oligogenic, and quantitative inheritance can be involved (3,13,20,30,31). In case the resistance in 'Kavkaz/K4500 l.6.a.4' would be largely quantitatively inherited, the detected virulence emphasizes that pathogen populations may also adapt to that form of resistance. In that case, quantitatively inherited resistance would not be necessarily durable. Obviously, abrupt circumvention of resistance by adaptation in the pathogen demonstrates the disadvantage of resistance conferred by one or a few genes with large effects, though quantitative resistance neither excludes specificity nor adaptation by pathogens (2,10,18,19,21, 22). Even if wheat cultivars have not been reported to unequivocally succumb to new pathotypes of the fungus (15), the present and previous (17) studies demonstrated specificity, and, thus, the potential of the pathogen to circumvent resistance in the host. However, adaptation of *M. graminicola* to resistance in the host by an increment of the frequency of individuals with appropriate virulence characteristics might be relatively slow, since it was strongly associated with the dissemination of such individuals. The rainsplash-dispersal of the asexual pycnidiospores during the growing season is relatively inefficient (28) as compared with the distribution of airborne propagules such as uredospores of rusts. Indeed, ascospores of *M. graminicola* are airborne and efficiently disseminated (27). They are of prime importance for the establishment of the disease in the young crop, but their contribution to the rate of an epidemic in a developing crop is unknown. Sudden epidemics are often associated with mutational events from avirulence to virulence and extended distribution of such clones, and are clearly demonstrated in pathogens with typically qualitative aspects of resistance and virulence or those that lack a generative stage (boom and bust) (2,10). In contrast, *M. graminicola* is a pathogen that is more characterized by quantitative aspects of resistance and virulence. In addition, it has a functional sexual cycle and a relatively inefficient mechanism of asexual spore dispersal during the growing season. Hence, a gradual deterioration of resistance rather than explosive epidemics should be expected. It is not surprising, therefore, that decline of resistance to *M. graminicola* often remains unobserved, and thus not reported, particularly when the commercial cultivation of cultivars is short. Nevertheless, examples such as the Dutch cultivar Obelisk, that was considered as resistant when released in 1985, and is currently among the most susceptible cultivars, emphasize that adaptation in the pathogen population should not be underestimated (1; G. H. J. Kema and C. H. Van Silfhout, *unpublished data*).

Pathogen isolates with a high σ^2_P, as well as isolates with a low σ^2_P and a high overall *P* level, might carry relatively large proportions of specific virulence factors. Such isolates are considered to be of importance as tester isolates in breeding for durable resistance (22). Hence, breeding cultivars durably resistant to *M. graminicola* should be preceded by a thorough pathogen survey to enable the selection and employment of such isolates.

Apart from the fact that similar conclusions applied to *N*, the difference between this parameter and *P*, as illustrated by dissimilarities of σ^2_P and σ^2_N, requires a comprehensive effort to elucidate its biological meaning.

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