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Genetic variation for foot-rot and *Fusarium* head-blight resistances among full-sib families of a self-incompatible winter rye (*Secale cereale* L.) population

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Abstract The amount of genetic variation for resistance to foot rot caused by *Pseudocercosporella herpotrichoides*, *Fusarium* spp., and *Microdochium nivale* and for resistance to head blight caused by *Fusarium culmorum* are important parameters when estimating selection gain from recurrent selection in winter rye. One-hundred and eighty-six full-sib families of the self-incompatible population variety Halo, representing the Petkus gene pool, were tested for foot-rot resistance at five German location-year combinations (environments) and for head-blight resistance in three environments with artificial inoculation in all but one environment. Foot-rot rating was based on 25 stems per plot scored individually on a 1–9 scale. Head-blight resistance was plotwise scored on a 1–9 scale and, additionally, grain-weight per spike was measured relative to the non-inoculated control plots. Significant estimates of genotypic variance and medium-sized heritabilities ($h^2 = 0.51$–0.69) were observed in the combined analyses for all resistance traits. In four out of five environments, the amount of genetic variance was substantially smaller for foot-rot than for head-blight rating. Considerable environmental effects and significant genotype-environment interactions were found for both foot-rot and head-blight resistance. Coefficients of error-corrected correlation among environments were considerably closer than phenotypic correlations. No significant association was found between the resistances to both diseases ($r = -0.20$ to 0.17). In conclusion, intra-population improvement by recurrent selection should lead to substantial higher foot-rot and head-blight resistances due to significant quantitative genetic variation within Halo. Selection should be carried out in several environments. Lack of correlation between foot-rot and head-blight resistance requires separate infection tests for improving both resistances.

Key words Quantitative resistance · *Pseudocercosporella herpotrichoides* · *Microdochium nivale* · *Fusarium culmorum* · Population parameter

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Introduction

Fusarium species are widespread soil-borne pathogens infecting winter rye (*Secale cereale* L.) at all host growth stages. In Germany, foot rot in wheat is mainly caused by *Pseudocercosporella herpotrichoides* (Fron) Deighton, and *Fusarium* species, especially *F. culmorum* (W.G.Sm.) Sacc., *F. graminearum* Schwabe, and *F. avenaceum* (Fries) Sacc., and *Microdochium nivale* (Fries) Samuels & Hallet (Duben and Fehrmann 1979). In winter rye, at least two of these species have been found in most locations simultaneously and could frequently be isolated from the same stems or even from the same necrotic lesions (Miedaner et al. 1993a). Resistance selection should, therefore, be directed towards the whole pathogen complex. Yield losses by foot rot are due to restricted nutrient and water transport and increased lodging. They are reported to amount to up to 45% depending on environment and the fungal species involved (Meyer 1985; Frauenstein 1987). Resistance is inherited quantitatively in hybrid rye material (Höxter et al. 1992; Miedaner et al. 1995a) and population varieties (Bojarczuk and Bojarczuk 1985), with no genotype being completely resistant or susceptible. This indicates that several genes control resistance (Geiger and Heun 1989). Similar results were obtained with head blight resulting from *F. culmorum* in winter rye (Miedaner et al. 1993 b, 1995 b). The most common *Fusarium* species causing head blight are *F. culmorum* and *F. graminearum*. Epidemic infections lead to considerable yield losses (Miedaner et al. 1993b),

increased seedling and foot-rot infection of the following crop (Duben and Fehrman 1980), and grain contamination with mycotoxins (Chelkowski 1989; Perkowski et al. 1995).

In hybrid rye breeding, population varieties are still important sources of variability for inbred-line development (Geiger 1985). For this purpose, they are either crossed directly with self-fertile material or improved previously by recurrent selection (Geiger 1988). Increasing the frequency of resistance genes in a breeding population also enhances the chance to select superior genotypes from it (Sprague and Eberhart 1977). To date, no data are available on the variation of resistances to foot rot and head blight within self-incompatible rye populations. Thus, the aim of the presented study was to (1) estimate the relative importance of genotypic variance and genotype-environment interaction variance, and (2) calculate the heritability for resistance to foot rot and head blight from multi-location tests of full-sib families from the widely grown population variety Halo.

Materials and methods

Plant material

Single plants from the self-incompatible, open-pollinated winter rye cultivar Halo were vegetatively cloned and two single plants with 10–20 clones each were crossed pairwise between isolation walls to obtain full-sib families. Halo represents the 'Petkus' gene pool, one of the major heterotic groups currently used in hybrid rye breeding (Geiger 1985). For all experiments, two sets of 93 full-sibs each, randomly chosen from a larger population, were used. Full-sib families were randomly assigned to the two sets.

Foot-rot resistance tests

Foot-rot resistance was tested in 1990 at Bergen near Celle (BER) and Klausheide near Münster (KLA) in northern Germany. In 1991, BER, KLA, and additionally the experimental station Oberer Lindenhof near Reutlingen (OLI) in southern Germany, were used. Each full-sib family was grown in one-row microplots of 1 m length with 0.42 m spacing between plots at a seed density of 320 kernels m^{-2}. The experiments were conducted utilizing two separate but adjacent 10 × 10-lattice designs with two replicates including seven standard varieties. Recommended cultural practices were used throughout the growing season at each location.

Genotypes were artificially inoculated by spreading dry, crushed wheat-grain material colonized with either *P. herpotrichoides* var. *acuformis* (BER90, BER91), an equidosal mixture of *F. culmorum* and *F. graminearum* (KLA91), or with *M. nivale* var. *nivale* (OLI91). At KLA90, genotypes were exposed to a natural soil-borne infection. Source and preparation of inoculum, and inoculation procedure were exactly the same as previously described (Miedaner et al. 1995a). At late-milk ripening, 25 randomly chosen stems per plot were harvested. Stems were thoroughly washed, the outer leaf sheaths removed, and the lower 10 cm of the stem base visually rated for foot rot on a 1–9 scale as follows: 1 = no lesion visible, 2 = lesion of pinpoint size, 3 = lesion covering less than one-fourth the circumference of the stem, 4 = lesion covering about one-fourth to half the circumference of the stem, 5 = lesion covering about half to three-fourths the circumference of the stem, 6 = lesion covering more than three-fourths the circumference of the stem, 7 = lesion girdling the stem, no softening of the tissue, 8 = lesion girdling the stem, moderate softening of the tissue, 9 = stem fully necrotic and softened. This scale describes both necrotization of the stems and softening of the tissue.

To evaluate disease incidence of the individual foot-rot fungi, necrotic lesions from 100 diseased stems per replicate and environment were cut out, surface-disinfected and incubated on agar as recently described by Miedaner et al. (1995a). The resulting colonies were identified according to their conidial morphology (Nirenberg 1981).

Head-blight resistance tests

The experiments with head-blight inoculation were grown in 1990 at Stuttgart-Hohenheim (HOH) and in 1991 at HOH and BER. At HOH, two-row microplots of 1 m length with 0.21 m spacing between rows and 0.42 m spacing to the neighboring plot were used. At BER, genotypes were grown in one-row microplots of 1.5 m length with 0.42 m spacing between plots. Each of the two sets was planted in two adjacent treatment blocks: non-inoculated vs inoculated. Plots within both treatment blocks were arranged according to a 10 × 10-lattice design including seven standard varieties. Recommended cultural practices were used throughout the growing season at each location.

Inoculum production and inoculation were performed as previously described (Miedaner et al. 1995b). Each genotype was artificially inoculated at its respective flowering time, and routinely for a second time 3 days later, with a mixture of four *F. culmorum* isolates. The inoculum consisted of a spore suspension with 0.5×10^6 spores per ml and was applied at a rate of 30 ml per row. At HOH, the field was sprinkled with a mist irrigation device in the morning after every inoculation from 7:00 to 12:00 h every 30 min for a period of 2-min each to ensure a high relative humidity. At BER91, no irrigation water was applied. Disease severity was rated four times at HOH and two times at BER on a 1–9 scale (1 = no symptoms to 9 = fully diseased, Mielke 1988). Two resistance traits – head-blight rating, averaged over all ratings with significant genotypic differentiation, and grain weight per spike relative to the non-inoculated plots – were assessed (Miedaner et al. 1993b).

Statistical analyses

Analyses of variance were based on single-plot data. The two sets can be considered as independent material replicates because the 93 full-sibs were randomly assigned to the sets. Analyses of variance across the five location-year combinations (environments) were based on lattice-adjusted entry means (Cochran and Cox 1957). For each environment, trait values and their residuals were normally distributed. Repeatability and broad-sense heritability estimates were based on entry means across replications (in individual environments) and across environments respectively (Wricke and Weber 1986; Falconer 1989). Coefficients of phenotypic correlations (r_p) between all pairs of environments were calculated using the established procedure (Falconer 1989). To exclude the error effects that mask the genotypic covariation between the two environments, coefficients of phenotypic correlation were corrected according to the following formula:

$$r_{ec} = \frac{\text{cov}\ (g_1 g_2) + \text{cov}\ (ge_1, ge_2)}{\sqrt{(\sigma^2 g_1 + \sigma^2 ge_1)}\sqrt{(\sigma^2 g_2 + \sigma^2 ge_2)}}$$

with r_{ec} = coefficient of error-corrected correlation, cov = covariance of the two environments 1 and 2 with the subscripts g or ge meaning genotypic or genotypic-environment covariance; σ^2_g, σ^2_{ge} = genotypic or genotype-environment interaction variance for environment 1 or 2, respectively. Any deviation of the coefficient of error-corrected correlation from a value of 1 is caused by genotype-environment interaction variance under the assumption that cov (ge_1, ge_2) is zero or at least considerably smaller than the respective variances. The standard errors of the error-corrected correlation coefficients were computed according to Mode and Robinson (1959). The same procedure was used to calculate error-corrected correlation coefficients between foot-rot and head-blight resistances for all pairs of environments. To demonstrate the theoretical frequency distributions of the genotypic values for the individual environments (see

Fig. 1), the respective means and genotypic standard deviations averaged over both sets of full-sibs were implemented in the function of normal distribution (Wricke and Weber 1986). All analyses of variance and coefficients of phenotypic correlation were carried out with the computer package PLABSTAT (Utz 1991a); estimations of covariance, coefficients of genotypic correlation and coefficients of error-corrrected correlation were computed with PLABCOV (Utz 1991b). The effects of sets, genotypes, environments, and replicates were assumed to be random variables.

Results

Foot-rot resistance

The five environments differed considerably in the incidence of *P. herpotrichoides*, *Fusarium* species, and *M. nivale* (Table 1). The artificially inoculated pathogens mostly dominated on the infected stems, although lesions were additionally caused by natural soil-borne inoculum. In the environment with natural infection (KLA90), *P. herpotrichoides* was isolated most frequently. This species occurred in four out of five locations together with high frequencies of *Fusarium* species. *M. nivale* was only found in higher amounts at OLI91 after artificial inoculation. Mean foot-rot rating ranged from 3.3 to 7.0, illustrating a medium to high disease severity in all environments. The two sets showed small differences, set 2 yielded lower levels of significance for genotypic differentiation at BER90 and KLA91. Apart from KLA91, set 2, genotypic variance was significant in all cases, reaching the 5% significance level in six out of ten environment-set combinations.

Significant genotypic variation across environments was observed for foot-rot rating in the combined analysis (Table 2). The effect of the sets was not important. Environment variance and genotype-environment interaction variance were highly significant. The estimate of heritability was medium sized.

Phenotypic correlations between environments pooled over the two sets were only weak, although significant (Table 3). By contrast, the error-corrected correlations were considerably higher and exceeded twice their standard error. The correlations between the years 1990 and 1991 at KLA and BER were not closer than for the other comparisons across years and locations. In the individual environments, low to moderate repeatabilities were obtained.

Table 2 Variance component estimates and heritability of foot-rot rating of two sets each with 93 full-sib families combined across five environments (*df* = degrees of freedom)

Source of variation	*df*	Foot-rot rating
Sets (S)	1	–[a]
Genotypes (G) within sets	184	0.027**
Environments (E)	4	2.028**
G × E within sets	736	0.020**
Error	824	0.073
Heritability		0.59

** Significant at probability level $P = 0.01$
[a] Negative estimate

Head-blight resistance

Artificial inoculation resulted in similar head-blight ratings in all three environments; relative grain-weight per spike was slightly higher at BER91 (Table 4). Significant genotypic variation was found throughout the experi-

Table 1 Incidence (percentage of infected stems) of *P. herpotrichoides* (PH), *F. culmorum* and *F. graminearum* (FC/FG), other *Fusarium* species (FUS), and *M. nivale* (MN) in four environments with, and one environment without, artificial inoculation (inoc.); mean foot-rot rating, and significance level of genotypic variances (σ_g^2, F-test) of two sets each with 93 full-sib families tested in these environments

Environment[a]	Inoc. pathogen(s)	Set no.	Isolated pathogen (%)				Mean foot-rot rating: score (1–9)[b]	σ_g^2
			PH	FC/FG	FUS	MN		
BER90	PH	1	98	29	22	2	5.4	**
		2	92	38	38	11	5.6	+
KLA90	–[c]	1	85	20	30	3	5.9	**
		2	87	11	40	4	6.0	**
OLI91	MN	1	22	7	19	72	3.3	+
		2	41	9	7	56	3.3	+
BER91	PH	1	56	30	52	0	4.4	*
		2	71	19	24	0	4.0	*
KLA91	FC/FG	1	30	85	15	0	6.8	**
		2	48	91	10	2	7.0	ns

ns, +, *,** Not significant, significant at probability levels $P = 0.1$, 0.05, and 0.01, respectively
[a] BER = Bergen, KLA = Klausheide, OLI = Oberer Lindenhof
[b] 1 = no lesion visible to 9 = stem fully necrotic and softened
[c] Natural infection

Table 3 Coefficients of phenotypic correlation (above diagonal), repeatabilities (diagonal, bold face) and coefficients of error-corrected correlation (below diagonal) for foot-rot rating among five environments pooled over two sets each with 93 full-sib families

Environment[a]	Environment				
	BER90	KLA90	OLI91	BER91	KLA91[b]
BER90	**0.23**	0.32**	0.25**	0.25**	0.41**
KLA90	0.54^{++}	**0.47**	0.31**	0.25**	0.37**
OLI91	0.68^{++}	0.72^{++}	**0.15**	0.17*	0.30**
BER91	0.66^{++}	0.49^{++}	0.64^{++}	**0.22**	0.25*
KLA91[b]	0.82^{++}	0.59^{++}	0.78^{++}	0.90^{++}	**0.29**

*, ** Significant at probability levels $P = 0.05$ and 0.01, respectively
$^{++}$ Estimate greater than twice its standard error
[a] BER = Bergen, KLA = Klausheide, OLI = Oberer Lindenhof
[b] Data from set 1 only, due to missing significant genotypic variance in set 2 (see Table 1)

Table 5 Variance component estimates and heritability of head-blight rating and relative grain weight per spike of two sets each with 93 full-sib families combined across three environments (*df* = degrees of freedom)

Source of variation	*df*	Head-blight rating	Relative grain weight per spike
Sets	1	0.001	–[a]
Genotypes (G) within sets	184	0.124**	19.600**
Environments (E)	2	0.347**	55.589*
G × E within sets	368	0.031**	27.406**
Error	484	0.133	28.517
Heritability		0.69	0.51

*,** Significant at probability levels $P = 0.05$ and 0.01, respectively
[a] Negative estimate

ments with medium-sized repeatabilities. The growing conditions for winter rye were about the same in all environments as illustrated by the size of the grain-weight per spike of the non-inoculated plots. Across all environments, the coefficient of phenotypic correlation between head-blight rating and relative grain weight per spike was $r = -0.60$ ($P = 0.01$) and the corresponding coefficient of genotypic correlation was $r = -0.81$ exceeding twice its standard error.

Genotypic variation was highly significant for both resistance traits across all environments (Table 5). The environment variances and genotype-environment interaction variances were also significant. Compared to the genotypic variance, genotype-environment interaction variance was more important for relative grain-weight per spike than for head-blight rating. Accordingly, heritability was higher for the latter. The two sets showed no differences for both resistance traits.

Phenotypic correlations between environments pooled over the two sets were highly significant, but moderate for head-blight rating and low for relative grain weight per spike (Table 6). Again, the values increased considerably when the coefficients of correlation were error-corrected.

Comparison of foot-rot and head-blight resistances

Quantitative genotypic variation was detected for both foot-rot and head-blight resistance in all individual environments. In four out of five environments, the amount of genetic variance among the 186 full-sibs was smaller for foot-rot than for head-blight resistance (Fig. 1). Genetic variance was obviously not influenced by the mean foot-rot rating achieved in the individual environments.

Correlation coefficients between foot-rot ratings of five environments and head-blight ratings of three environments were not significantly different from zero for the 186 tested full-sibs in any set for any combination of environments. Coefficients of phenotypic correlation ranged from $r = -0.20$ to $r = 0.17$. Error-correction did not improve the correlation coefficients ($r = -0.32$ to 0.31).

Table 4 Means, significance levels of genotypic variance (σ_g^2, F-Test), and repeatabilities of head-blight rating and relative grain weight per spike in *F. culmorum* inoculated plots and means of grain weight per spike in non-inoculated plots for two sets each with 93 full-sib families tested in three environments

Environment[a]	Set no.	Head-blight rating (1–9)			Grain wt. per spike	Relative grain weight per spike		
		Mean	σ_g^2	Repeatability	Mean	Mean	σ_g^2	Repeatability
HOH90	1	3.0	**	0.58	1.90	71.0	**	0.54
	2	3.0	**	0.42	1.88	72.8	**	0.53
HOH91	1	4.2	**	0.51	1.70	71.1	**	0.54
	2	4.2	**	0.40	1.71	69.8	**	0.59
BER91	1	3.6	*	0.22	1.77	81.3	**	0.34
	2	3.7	**	0.43	1.75	84.9	**	0.47

*, ** Significant at probability levels $P = 0.05$ and 0.01, respectively
[a] HOH = Hohenheim, BER = Bergen

Table 6 Coefficients of phenotypic correlation (r_p) and error-corrected correlation (r_{ec}) among three environments for head-blight rating and relative grain weight per spike pooled over two sets each with 93 full-sib families

Correlated environments[a]	Head-blight rating		Relative grain weight per spike	
	r_p	r_{ec}	r_p	r_{ec}
HOH90-HOH91	0.48**	0.81^{++}	0.34**	0.44^{++}
HOH90-BER91	0.41**	0.69^{++}	0.21*	0.26^{+}
HOH91-BER91	0.41**	0.71^{++}	0.24**	0.37^{++}

*,** Significant at probability levels $P = 0.05$ and 0.01, respectively
$^{+}$, $^{++}$ Estimate greater than once and twice its standard error, respectively
[a] HOH = Hohenheim, BER = Bergen

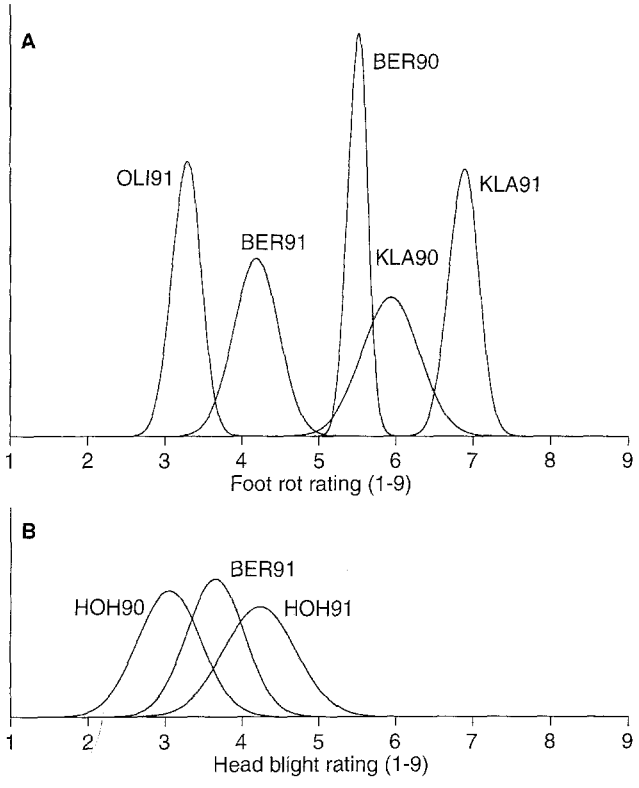

Fig. 1 Theoretical frequency distributions of genotypic values of foot-rot rating (**A**) and head-blight rating (**B**), estimated from means and genotypic standard deviations of 186 full-sib families tested in five environments for foot-rot resistance and in three environments for head-blight resistance, respectively. Foot rot and head blight were rated on 1–9 scales (see text). OLI = Oberer Lindenhof, BER = Bergen, KLA = Klausheide, HOH = Hohenheim

Discussion

With the exception of the experiment at KLA90, all resistance tests reported were performed with artificial inoculation techniques. However, in the foot-rot tests not only the inoculated pathogen but also a natural soil-borne inoculum played an important role as illustrated by the incidence of the major foot-rot pathogens when lesions were plated on agar. *P. herpotrichoides* dominated at most tests sites and was frequently isolated together with *Fusarium* species. In contrast to earlier findings (Miedaner et al. 1993a), *M. nivale* was isolated in higher proportions only at OLI91, a test site in the Swabian Highlands where this pathogen was artificially inoculated. Foot rot is obviously caused by several genera of pathogenic fungi (Duben and Fehrmann 1979; Miedaner et al. 1993a, 1995a), each with different optimal conditions for growth and infection. This probably explains the widespread occurrence of foot-rot disease in winter rye and the impossibility to define any common climatic conditions that favour infection in Middle Europe.

Ratings on a 1–9 scale as used in all experiments detected significant quantitative genotypic variation for both resistances. The assessment of yield components was not successful for the environments with foot-rot inoculations, because the non-inoculated control plots were infected by natural soil-borne inoculum to a similar extent as the artificially infected plots. By contrast, head blight by *F. culmorum* resulted in a significant reduction of grain weight per spike and a similar genotypic differentiation for head-blight rating. In the combined analysis, however, genotype-environment interaction variance for relative grain-weight per spike amounted to 21% of the total variance but only to 5% for head-blight rating. The relative proportion of the other sources of variance on total variance were of about the same for both resistance traits. Rating head-blight symptoms two to three times during disease progress should suffice for selection due to the high genotypic correlation between both resistance traits. Head-blight rating is a much faster procedure and affords less experimental effort than cutting 20 heads per row from inoculated and non-inoculated plots by hand to assess relative grain weight per spike.

The representative sample of 186 full-sib families from the Petkus population Halo expressed significant genetic variation for foot-rot and head-blight resistances. This agrees with experimental results reported for these pathosystems in rye with different genetic materials (Bojarczuk and Bojarczuk 1985; Höxter et al. 1992; Miedaner et al. 1993a, b, 1995a, b). Comparing the reported results with foot-rot ratings from 16 single-cross hybrids tested in four environments in parallel with the full-sibs showed that full-sibs expressed half the genetic variance of single-cross hybrids (Fromme, unpublished). This is caused by the high variability within full-sibs and is in accordance with population genetic theory (Wricke and Weber 1986). Genotype-environment interaction variance, however, was considerably smaller for full-sibs than for single-cross hybrids illustrating the higher phenotypic stability of heterogeneous rye genotypes.

Estimates of population parameters can be compared for both resistances, because the same full-sib

families were tested using ratings on a 1–9 scale for both disease resistances and the mean values of the ratings were of comparable size. Interestingly, the amount of variance found within Halo in four out of five environments was lower for foot-rot than for head-blight resistance (Fig. 1). Across all environments, the genotypic variance component for head-blight resistance was 4.5-times greater than for foot-rot resistance. Because the population was not preselected for either resistance, this result may reflect substantial differences in genetic variation in the Petkus gene pool. However, smaller genotypic variance for foot-rot resistance may partly be caused by a correlated gain from selecting against lodging over several cycles of recurrent selection. It should be noted, that the estimation of these parameters depends highly on the test environment (Falconer 1989). These were partly different for both resistances in this study. Genotype-environment interactions were important for both foot-rot and head-blight resistances. The causal fungi of both diseases strongly interact with environmental factors and the genotype-environment interaction of the host itself additionally increases this source of variance. This corroborates results from other field studies on foot-rot resistance in winter rye (Miedaner et al. 1995a), as well as *Fusarium* head-blight resistance in rye (Miedaner et al. 1993b, 1995b) and in wheat (Snijders 1990). Accordingly, phenotypic correlations among test environments in this study were low. However, error-corrected correlations were much closer, illustrating the high proportion of error variance on total variance that masks the genotypic covariation among environments in full-sibs.

No association between both foot-rot and head-blight resistance was found. The correlation might be underestimated because both resistances were assessed in partly different environments and foot rot was caused by at least two different pathogen species (Table 1), while head blight was attributable only to *F. culmorum*. Nevertheless, even for the comparisons with KLA91, where *Fusarium* species were isolated from nearly all foot-rot lesions (Table 1), no significant associations could be found ($\bar{r} = -0.16$). The error-corrected correlations were of similar low values as for the other comparisons. Hence, strong host growth stage and/or host organ specifities have to be considered for the pathosystems analyzed. Highly significant genotype-growth stage interaction for *F. culmorum* and *F. graminearum* has already been reported among earlier growth stages (from three-leaf to jointing stage) tested under controlled environment conditions (Höxter et al. 1992).

The population variety Halo represents one of the major heterotic groups currently used in hybrid rye breeding. Due to ample quantitative genotypic variation found for both foot-rot and head-blight resistance, recurrent selection should result in considerable intra-population improvement. Resistance tests can be easily integrated in the recurrent selection scheme using full-sibs as proposed by Geiger (1988). In this scheme, seed production by pair-wise crossings of vegetatively cloned single plants in year 1 is followed by a pre-test for traits with high heritabilities and further seed multiplication in year 2. Finally, agronomic performance is tested in 3–5 environments in year 3. Considering heritability estimates and financial costs for disease assessment, head-blight resistance could be tested as early as year 2, while the time consuming foot-rot rating should be delayed until year 3, when population size is already reduced by selection. Large genotype-environment interaction variances and the widely differing fungal populations in individual test sites permit selection in several environments. The high coefficients of error-corrected correlation beween environments, however, show that then a substantial environmental covariance can be used by the rye breeder in recurrent selection. Considering the missing covariance between foot-rot and head-blight resistance, no indirect selection gain can be expected from improving one of them.

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