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Determining environmental covariates which explain genotype environment interaction in winter wheat through probe genotypes and biadditive factorial regression

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Abstract Genotype-environment interaction has been analyzed in a winter-wheat breeding network using biadditive factorial regression models. This family of models generalizes both factorial regression and biadditive (or AMMI) models; it fits especially well when abundant external information is available on genotypes and/or environments. Our approach, focused on environmental characterization, was performed with two kinds of covariates: (1) deviations of yield components measured on four probe genotypes and (2) usual indicators of yield-limiting factors. The first step was based on the analysis of a crop diagnosis on four probe genotypes. Difference of kernel number to a threshold number (DKN) and reduction of thousand-kernel weight from a potential value (RTKW) were used to characterize the grain-number formation and the grain-filling periods, respectively. Grain yield was analyzed according to a biadditive factorial regression model using eight environmental covariates (DKN and RTKW measured on each of four probe genotypes). In the second step, the usual indicators of yield-limiting factors were too numerous for the analysis of grain yield. Thus a selection of a subset of environmental covariates was performed on the analysis of DKN and RTKW for the four probe genotypes. Biadditive factorial regression models involved environmental covariates related to each deviation and included environmental main effect, sum of water deficits, an indicator of nitrogen stress, sum of daily radiation, high temperature, pressure of powdery mildew and lodging. The correlations of each environmental covariate to the synthetic variates helped to discard those poorly involved in interaction (with | correlation | <0.3). The grain yield of 12 genotypes was interpreted with the retained covariates using biadditive factorial regression. The models explained about 75% of the interaction sums of squares. In addition, the biadditive factorial regression biplot gave relevant information about the interaction of the genotypes (interaction pattern and sensitivities to environmental covariates) with respect to the environmental covariates and proved to be interesting for such an approach.

Key words Genotype-environment interaction · Biadditive factorial regression · Biplot · Crop diagnosis · Probe genotypes · Winter wheat

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Introduction

Plant breeders have to deal with genotype*environment interaction in most of their multilocal experiments. In plant breeding, a huge literature is devoted to the statistical models for analyzing genotype*environment interaction (Freeman 1973; Denis and Vincourt 1982; Lin et al. 1986; Westcott 1986; Becker and Léon 1988; Ceccarelli 1989; Crossa 1990; Freeman 1990; Gauch 1992; Romagosa and Fox 1993; van Eeuwijk et al. 1996; Kang and Gauch 1996; Brancourt-Hulmel et al. 1997). Especially when additional information is available, factorial regressions or biadditive factorial regressions are of interest. Biadditive factorial regression generalizes both factorial regression (Denis 1988) and AMMI (Gollob 1968; Gauch 1992). Just as for AMMI, synthetical environmental variates, or axes, are built, but under the restrictions of being linear combinations of environmental variates. Applied to a set of environmental variates, Wood (1976) showed how to find several linear functions to explain the interaction. Such a model can be extended to covariates related to both factors, i.e. genotype and environmental factors. A general presentation of these models has been given by Denis (1988, 1991).

Some literature is also devoted to the relationships between the instability of grain yield and the instability of yield components (Sierts et al. 1987; Baril 1992; Nachit et al. 1992; Simane et al. 1993; Jackson et al. 1994; Biarnès-Dumoulin et al. 1996). Explaining genotype*environment interaction observed on grain yield is a real challenge as grain yield results from complex compensations between yield components. Prihar and Steward (1990) recommended an analysis of the harvest index, defined as the ratio of grain yield to the above-ground biological yield, for screening cultivars. As this criterion is affected by environmental constraints, they stated that fair intercrop or intercultivar comparisons should be based on the estimated genetic harvest index for a given environment. They proposed a procedure using an upper-bound slope through the origin to estimate such a genetic harvest index. According to their model, the highest yields related to a given dry matter correspond to the upper-bound slope and to least-stressed and/or stress-adapted plants. Such an approach could be adapted to the analysis of yield components. In winter wheat, grain yield comes from two main yield components determined over two distinct periods: kernel number per square meter (KN) and thousand-kernel weight (TKW). Kernel number describes the time-period before flowering while TKW characterizes the grain-filling period. A way to estimate potential values for KN and TKW has been proposed (Brancourt-Hulmel et al. 1999) and referred to a crop diagnosis (Sebillotte 1980; Doré et al. 1997). Plants free from stress or well-adapted to it would produce yield components close to the potential values. This can be applied to a specific set of genotypes, also termed as probe (or reference) genotypes (Cooper and Fox 1996; Desclaux 1996; Brancourt-Hulmel et al. 1999).

In France, climatic conditions are very diverse within a given series of trials for wheat. This complicates the characterization of the environments and, therefore, the statistical analysis of interaction. Covariates are countless and every one explains almost nothing. Linear regression models are not adapted to integrate numerous covariates because they demand many parameters, in contrast biadditive factorial regression is much more parsimonious.

Environmental characterization can be achieved directly by the measurement of environmental variables, which can be physical, biological or nutritional, or indirectly by measurement of plant responses to capture the influence of environmental conditions on plant performance. For the indirect characterization of the environments in winter-wheat trials, analysis of the interaction on probe genotypes can help to assess with more insight the effect of environmental factors on the formation of yield, particularly during grain-number formation and grain-filling periods (Brancourt-Hulmel 1999).

In the context of an environmental characterization with probe genotypes, linear factorial regression helped to explain the genotype*environment interaction observed for the yield of winter wheat (Brancourt-Hulmel 1999). When the variates are too numerous, this model takes into account a small proportion of variates. In order to introduce more covariates, biadditive factorial regression has to be investigated. In this context, the aim of this paper is: (1) to determine appropriate environmental covariates with the help of probe genotypes; (2) to select environmental covariates when they are too numerous; and (3) to use these covariates for interpreting the genotype by environment interaction on the whole set of genotypes. Two kinds of environmental covariates are investigated: deviations of yield components measured on probe genotypes and usual indicators of yield-limiting factors. The breeder is interested in both approaches. With the first covariates, it is possible to compare the behavior of a given genotype to one or several well-known genotypes (probe genotypes for instance) while the sensitivity of the genotypes to yield-limiting factors can be measured with the second.

Materials and methods

Experimental data

Data were also reported in a previous paper (Brancourt-Hulmel 1999). Experiments were carried out at five INRA (France) research stations in 1991 and 1992. The environments were combinations of 2 years (1991, 1992) by six INRA location*treatment combinations [Mons (MON*IN), Rennes (REN*IN), La Minière (MIN*IN), Dijon (DIJ*IN and DIJ*S2); IN is the standard agronomic treatment meanwhile S2 is a late sowing date].

The experiment was divided into two sets of genotypes, both of them being tested in all 12 environments. The first one was a set of four probe genotypes and was devoted to the assessment of deviations of yield components: Talent (TAL), Soissons (SOI), Camp-Rémy (CAR) and Arminda (ARM). These probe genotypes show very distinct earliness. Earliness was the most important criterion for their choice because it enhanced diverse patterns for the formation of grain yield. These genotypes differed also for susceptibilities to diseases or to lodging. A second set of 12 genotypes, independently tested, [Apollo (APO), Artaban (ART), Baroudeur (BAR), Camp-Rémy (CAR), Génial (GEN), Récital (REC), Renan (REN), Rossini (ROS), Soissons (SOI), Talent (TAL), Thésée (THE), and Viking (VIK)], was devoted to the analysis of grain yield. They were commonly grown cultivars in France at that time, and differed greatly for grain yield, earliness at heading, susceptibilities to diseases or to lodging. Three of them were tested twice as they were common to the subset of probe genotypes. More details about the experiment, such as characteristics of the genotypes or the environments, plant sampling and measurements, are reported in Brancourt-Hulmel (1999).

Definition of environmental covariates

Environmental covariates were of two kinds : (1) deviations of yield components measured on probe genotypes and (2) usual indicators of yield-limiting factors.

Assessing deviations from potential values (DKN and RTKW) of the four probe genotypes

In each experimental plot, grain yield (GY) and the thousand-kernel weight (TKW) were measured. The kernel number per square meter (KN) was deduced from the relationship between grain yield and the yield components: GY=KN*TKW. In each environment and for each probe genotype, two outputs from crop diagnosis were determined from the theoretical function of TKW

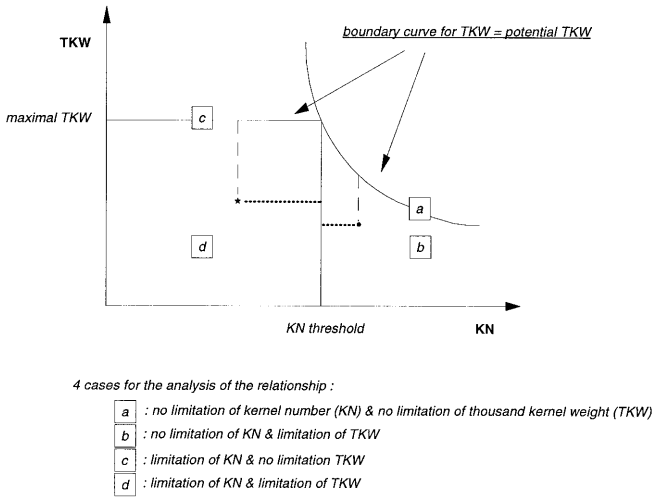

Fig. 1 Determination of reduction of thousand-kernel weight (RTKW symbolized by a *large dashed line*) and difference of kernel number (DKN in a *narrow dashed line*) for two examples. Figure adapted from Leterme et al. (1994)

with respect to KN (see Fig. 1): DKN – the difference of kernel number (from the threshold) – is defined by 100* (*KNthreshold–KN*)/*KNthreshold*; and RTKW – the reduction of thousand-kernel weight (from the potential) – is defined by max[0;100*[*potentialTKW–TKW*)/(*potentialTKW*].

KNthreshold and *potentialTKW* have been determined from a long-term experiment carried out since 1987 and gathering 500 yield components per genotype on average (Brancourt-Hulmel et al. 1999). Determination of *KNthreshold* and *potentialTKW* requires both experiments and time, and were only available for the four probe genotypes. This explains the two sets of genotypes in our study. DKN characterizes grain-number formation: a positive value means that kernel number is smaller than the threshold and could have been affected by environmental factors, while a negative value indicates that kernel number is sufficient to produce maximal grain yield. The reduction of kernel number, RKN, is a slightly different variate which could be defined for the formation of kernel number. For this variate, only positive values are taken into account, the negative ones being forced to zero (Brancourt-Hulmel et al. 1999). When negative values are forced to zero, bias could have been introduced for the evaluation of favorable environments; thus DKN is preferred to RKN. RTKW accounts for the grain-filling. Environments were free from stress for the grain-filling period when TKW was equal to the potential (Fig. 1). When, due to experimental error, observed TKW is higher than the as-

Table 1 Deviations (in %) from *KNthreshold* (a) from *potentialTKW* (b) for the four probe genotypes in each environment

a

Environments	TALdkn	SOldkn	CARdkn	ARMdkn	Mean	std	snk grouping at 0.05 probability level
91RENIN	–31.4	–20.3	–15.0	– 5.3	–18.0	10.9	*
91MININ	–15.9	–11.3	– 4.3	–12.2	–10.9	4.8	*
91DIJIN	2.7	3.6	1.4	0.5	1.8	1.8	*
92DIJS2	4.2	9.8	10.6	8.0	8.2	2.8	* *
91DIJS2	3.6	12.5	5.5	13.8	8.9	5.1	* *
91MONIN	0.5	14.5	18.9	13.1	11.8	7.9	* *
92MININ	0.9	6.0	28.9	11.9	11.9	12.2	* *
92RENIN	12.5	– 0.4	18.2	17.9	12.1	8.7	* *
92DIJIN	2.4	13.8	15.6	20.9	13.2	7.8	* *
91ONDIN	– 2.9	23.1	14.4	29.6	16.1	14.1	* *
92MONIN	14.4	22.7	15.8	18.2	17.8	3.6	* *
92ONDIN	5.0	23.6	22.6	30.8	20.5	11.0	*
Mean	– 0.3	8.1	11.1	12.2	7.8		
std	12.4	13.7	12.3	13.1			
snk grouping at 0.05 probability level	*	*	*	*			

b

	SOlrtkw	CARrtkw	ARMrkw	TALrtkw			
91MININ	6.0	13.2	16.8	11.3	11.8	4.5	*
92DIJIN	16.7	19.6	13.6	23.8	18.4	4.3	*
91RENIN	15.1	13.3	31.7	14.5	18.7	8.7	*
91DIJIN	19.4	18.8	19.9	17.0	18.8	1.3	*
91MONIN	18.3	13.1	20.1	27.4	19.7	5.9	* *
92DIJS2	18.3	15.9	24.1	22.7	20.3	3.8	* *
91DIJS2	20.0	22.9	20.6	23.3	21.7	1.6	* *
92ONDIN	21.3	24.4	7.4	35.6	22.2	11.6	* *
92MONIN	20.0	22.4	24.0	28.5	23.7	3.6	* *
92MININ	21.6	19.1	37.6	29.1	26.9	8.3	* *
91ONDIN	27.0	36.4	22.4	32.6	29.6	6.2	* *
92RENIN	22.3	26.1	36.4	41.0	31.5	8.7	*
Mean	18.8	20.4	22.9	25.6	21.9		
std	5.0	4.1	8.4	7.0			
snk grouping at 0.05 probability level	*	*	*	*			

sessed potential, RTKW is forced to zero. Below the potential value, TKW was limited by a number of factors. Leterme et al. (1994) indicated how to interpret the different cases shown in Fig. 1. Eight environmental covariates were provided as each variate was calculated for each probe in each environment: ARMdkn, CARdkn, SOIdkn, TALdkn for the difference of kernel number, and ARMrtkw, CARrtkw, SOIrtkw and TALrtkw for the reduction of thousand kernel weight (Table 1).

Usual indicators of yield-limiting factors

The usual environmental covariates are physical, biological or nutritional; they were determined for the main two periods of the cycle of wheat: (1) during grain-number formation (before flowering) and (2) during grain-filling (after flowering). Indications for the two periods have been marked by the letters "K" (for kernel number) and "T" (for thousand-kernel weight) in the last position of the codes, respectively. For instance, "LodgK" and "LodgT" stand for lodging assessed in the two periods. Codes are given below, between brackets.

For the first period, the following covariates were used: sum of daily water deficits (ETm-ETa) from the ear at 1 cm to flowering (WDK), ratio between total nitrogen absorbed by the plant and kernel number (BK), sum of daily radiation from the ear at 1 cm to flowering (RK), sum of daily radiation ±3 days at meiosis [RKm], infection of powdery mildew (PMK) and pressure of lodging (LodgK). BK was used to indicate nitrogen stress. During winter, the minimum daily temperature was never below –4°C.

For the grain-filling period the covariates are: sum of daily water deficit, (WDT), daily radiation (RT), high temperature estimated by the sum of degree-days based on 25°C (HTT), infection of powdery mildew (PMT) and pressure of lodging (LodgT). For this period, all climatic variates are calculated from flowering to maturity. Visual development of diseases was observed on all the genotypes. The development of disease in each location was described by the maximum scores noted on a given genotype (whether probe genotype or not) and other indicators were calculated according to the cycle of each probe genotype. Simple statistics on these environmental covariates are shown in Table 2. For more details about the determination of these variates, see Brancourt-Hulmel et al. (1999).

In addition, the environmental main effect (EFFECT) was used as environmental covariate in the approach, as done in joint-regression models (Finlay and Wilkinson 1963).

Statistical analysis

Genotype-environment interaction was first analyzed according ANOVA and the classical biadditive (AMMI) model involving up to three multiplicative terms. Definitions of these models can be found, for instance, in Brancourt-Hulmel et al. (1997). The previous environmental covariates were introduced into a biadditive factorial regression model, also termed as reduced rank factorial regression by van Eeuwijk (1995). It is written here with three multiplicative terms:

$$E[Y_{ge}] = \mu + \alpha_g + \beta_e + \lambda_1\gamma_{g1}\left(\sum_{h=1}^{H^B}\delta_{h1}E_{eh}\right) + \lambda_2\gamma_{g2}\left(\sum_{h=1}^{H^B}\delta_{h2}E_{eh}\right) + \lambda_3\gamma_{g3}\left(\sum_{h=1}^{H^B}\delta_{h3}E_{eh}\right),$$

where $E[Y_{ge}]$ is the expectation of performance Y_{ge} for genotype g grown in environment e; μ is the general mean; α_g, is the genotype main effect; β_e is the environment main effect. Each of the multiplicative terms has the same structure: λ_* is the size, γ_{g*} is the normalized genotype vector of the genotype sensitivities, $\sum_{h=1}^{H^B}\delta_{h*}E_{eh}$ is a normalized linear combination of the H^B environmental covaria-

Table 2 Mean and range of limiting factor indicators for kernel-number elaboration period and grain-filling period from the 12 environments. Scale for powdery mildew and lodging: 1 (without infection or pressure) to 9 (heavily damaged)

	Symbol	Unit	Mean	std	Min	Max	
Formation of grain number							
Climatic variates							
Water deficit	$\Sigma(ETm–ETa)$ from ear at 1 cm to flowering	WDK	*mm*	11.3	17.4	0.0	46.6
Temperature	Number of days with minimum daily temp <4°C			No frost			
Radiation	Radiation days ±3 days at meiosis	RKm	MJ/m^2	14.6	2.6	8.2	17.8
	Radiation days from ear at 1 cm to flowering	RK	MJ/m^2	112.9	12.1	93.7	133.9
Diseases							
Powdery mildew		PMK	Score	1.5	0.7	1.0	3.2
Lodging		LodgK	Score	1.2	0.3	1.0	1.9
Nitrogen status							
	Nitrogen absorbed/ kemel number	BK	*mg/grain*	1.27	0.13	1.08	1.47
Grain-filling period							
Climatic variates							
Water deficit	$\Sigma(ETm–ETa)$ from flowering to maturity	WDT	*mm*	19.4	24.8	0.0	68.7
High temperature	Degree days from flowering to maturity based on 25°C	HTT	*°C*	28.9	14.6	10.1	55.9
Radiation	Radiation days from flowering to maturity	RT	MJ/m^2	68.6	4.5	58.1	74.9
Diseases							
Powdery mildew		PMT	Score	1.9	1.6	1.0	5.5
Lodging		LodgT	Score	2.6	2.2	1.0	7.5

tes, E_{eh}, assigned to the term. Similarly to standard biadditive models, identifiability between multiplicative terms is obtained by orthogonality constraints.

All statistical analyses were realized with the BIAREG package – set of Splus-functions – developed by Denis (1998), and available on request to the second author of the present paper. The environmental covariates were first centered and then scaled to unit variance.

Interpretation of biadditive factorial regression from the environmental viewpoint

We propose to interpret biadditive factorial regression from the environmental viewpoint via the correlations between the synthetic variates, $\sum_{h=1}^{H^B} \delta_{h1} E_{eh}$, $\sum_{h=1}^{H^B} \delta_{h2} E_{eh}$ and $\sum_{h=1}^{H^B} \delta_{h3} E_{eh}$, and the H^B initial environmental covariates, E_{eh}. These correlations will be displayed in Cartesian diagrams as in principal component analysis. Van Eeuwijk (1995) proposed a similar approach with the use of a reduced rank regression biplot containing three types of vectors whose coordinates are determined by the genotypic sensitivities, the environmental characterizations and coefficients for the environmental covariates within the reduced rank factorial regression axes. Environmental characterizations result from the linear combinations of the true environmental covariates provided by the model. In order to clarify such a biplot, we considered these three types of vectors with two separate plots, one containing the genotypic sensitivities and the coefficients of the environmental covariates, and the other containing the same genotypic sensitivities and the environmental characterizations. Ter Braak and Looman (1994) discussed several aspects of the biplot technique in reduced-rank regression, such as displaying qualitative regressor variables in the biplot, focusing the biplot analysis on the effects of a particular subset of regressors, and scaling the biplots.

In correlation scaling, the plots are proposed with vectors to underline the fact the interpretation must be done in term of the cosine of the angles and length of the vectors, and not in term of distances between the points. For instance, two opposite vectors are equivalent because their cosine (correlation) is –1; see Gower and Hand (1996) for more details about the use of this kind of representation.

Results

ANOVA and deviations of yield components

Genotype*environment interaction was significant for grain yield (Table 3a). Yields of the genotypes in the different environments differed greatly as shown in Fig. 2. Genotype mean yields varied from 64.5 to 75.1 q/ha (at 0% moisture content) and environments yielded from 64.4 to 89.6 q/ha on average. Four genotypes showed

Table 3 ANOVA tables for grain yield on the 12 genotypes. Interactive model (a). Partitioning of interaction with AMMI model (b), biadditive factorial regression with deviations of yield components (c) and usual indicators (d)

Interactive model

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	
a					
Genotype (G)	11	1604.2	145.8	25.9	*
Environment (E)	11	7540.7	685.5	121.8	*
G*E	121	3168.8	26.2	4.7	*
Pure residual	143	804.8	5.6		

Partitioning of interaction

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*		Efficiency (% of SSI[a])
b						
G*E	121	3168.8	26.2	4.7	*	100.0
1st term	21	1245.9	59.3	10.5	*	39.3
2nd term	19	730.1	38.4	6.8	*	23.0
3rd term	17	525.1	30.9	5.5	*	16.6
Remainder	64	667.7	10.4	1.8	*	
c						
G*E	121	3168.8	26.2	4.7	*	100.0
1st term	18	1235.3	68.6	12.3	*	39.0
2nd term	16	698.8	43.7	7.8	*	22.0
3rd term	14	518.7	37.1	6.6	*	16.4
Remainder	73	716.1	9.8	1.8	*	
d						
G*E	121	3168.8	26.2	4.7	*	100.0
1st term	20	1176.6	58.8	10.5	*	37.1
2nd term	18	689.9	38.3	6.8	*	21.8
3rd term	16	483.5	30.2	5.4	*	15.3
Remainder	67	818.8	12.2	2.2	*	

* Significant at the 0.05 probability level
[a] SSI: sum of squares of interaction

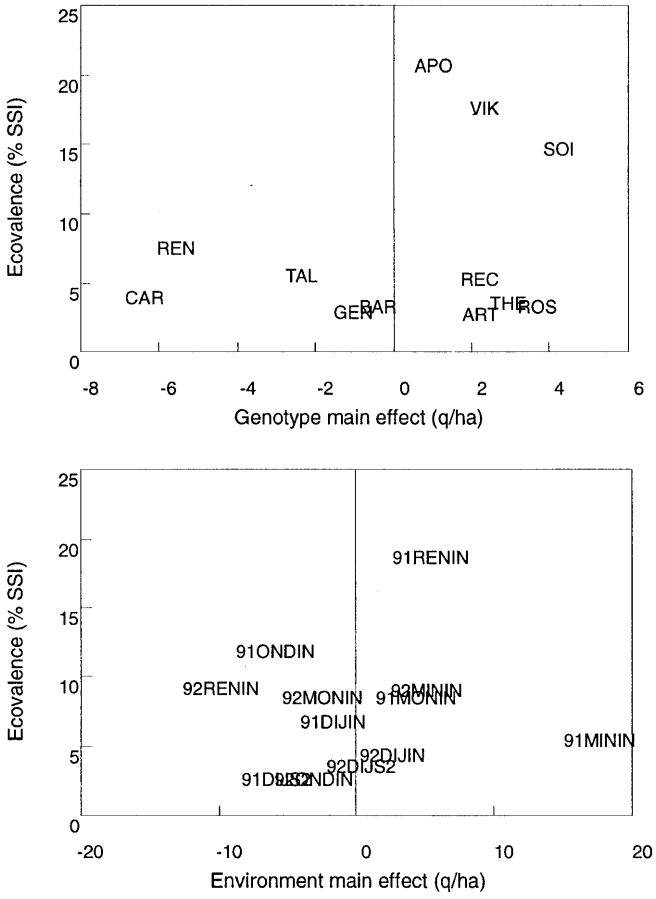

Fig. 2 Ecovalences and main effects for the genotypes (**a**) and the environments (**b**)

high ecovalences (Fig. 2a) and contributed the most to the interaction: APO (21.4%), VIK (18.3%), SOI (15.5%) and REN (8.3%) to a less extent. Six environments out of twelve were the most interactive (Fig. 2b): 91RENIN (19.4%), 91ONDIN (12.6%), 92RENIN (9.9%), 92MININ (9.9%), 91MONIN (9.2%) and 92MONIN (9.2%).

Great differences were observed for deviation of kernel number (DKN) in Table 1a. A positive value meant that environments were unfavorable during the grain-number formation. This is the case at 92ONDIN (20.5%) or at 92MONIN (17.8%). At 91RENIN and 91MININ the situation was more favorable as indicated by the negative values (–18.0% and –10.9% respectively). The interaction effect was also important for DKN: TAL scored –31.4% at 91RENIN while ARM gave 30.8% at 92ONDIN. For the reduction of thousand-kernel weight (RTKW), a similar pattern can be noted (Table 1b). Some environments were unfavorable during the grain-filling period (92RENIN and 91ONDIN) while only one environment was almost free from stress (91MININ). For interaction, extreme values varied from 6.0% for SOI at 91MININ to 41% for TAL at 92RENIN.

Table 4 Correlations of the eight environmental variates to the three synthetic variates

Environmental covariate	1st synthetic variate	2nd synthetic variate	3nd synthetic variate
TALdkn	–0.46	0.15	0.20
SOldkn	–0.38	0.57	0.05
CARdkn	0.02	0.41	–0.07
ARMdkn	0.35	0.36	0.53
TALrtkw	–0.47	0.15	0.52
SOlrtkw	–0.20	0.24	0.38
CARrtkw	0.29	0.15	0.31
ARMrtkw	0.53	0.34	–0.50

Deviations of yield components as environmental covariates

Using deviations of yield components as environmental covariates in a biadditive factorial regression with three terms (or synthetic variates), the sum of squares of interaction (SSI) was partitioned by 77.4% (Table 3c). The efficiency of this model for explaining the interaction is similar to AMMI which partitioned 78.9% of SSI with 3 terms (Table 3b).

The contributions of the eight variates to synthetic variates are not similar. Some correlations are stronger (over 0.5 or below –0.5) for SOIdkn, TALrtkw, ARMdkn and ARMrtkw (Table 4). SOIdkn is better correlated to the first and second axes while the three others are better correlated to the first and third ones. The other variates are more or less correlated to all three axes (SOIrtkw, CARrtkw, TALdkn) or to only one (CARdkn). It is therefore necessary to consider the three axes in the following graphical analyses.

Figure 3 displays biadditive factorial regression biplots with multiplicative parameters of the genotypes and coefficients for the environmental covariates. Just as for the AMMI model, points near the origin have little interaction while points distant from it are very interactive. APO, VIK, SOI and REN which were already highlighted in terms of ecovalence (Fig. 2a) are also highlighted in Fig. 3a. In addition, points near each other display similar interaction patterns (ART, THE, REC, TAL) while points distant from each other are different. APO, VIK and SOI are interactive and show different interaction patterns while the behavior of REN is more similar to that of APO. This is partly true as only 61% of SSI is captured by the two first synthetic variates. Then a third synthetic variate has to be considered. Figure 3b displays genotype parameters and environment characterizations: six environments are distant from the origin and contributed the most to the interaction: 91RENIN, 91ONDIN, 92RENIN, 92MININ, 91MONIN and 92MONIN. Environmental ecovalences already pointed out the same environments (Fig. 2b) but no information was given about the interaction pattern. On this plot, some of these environments are

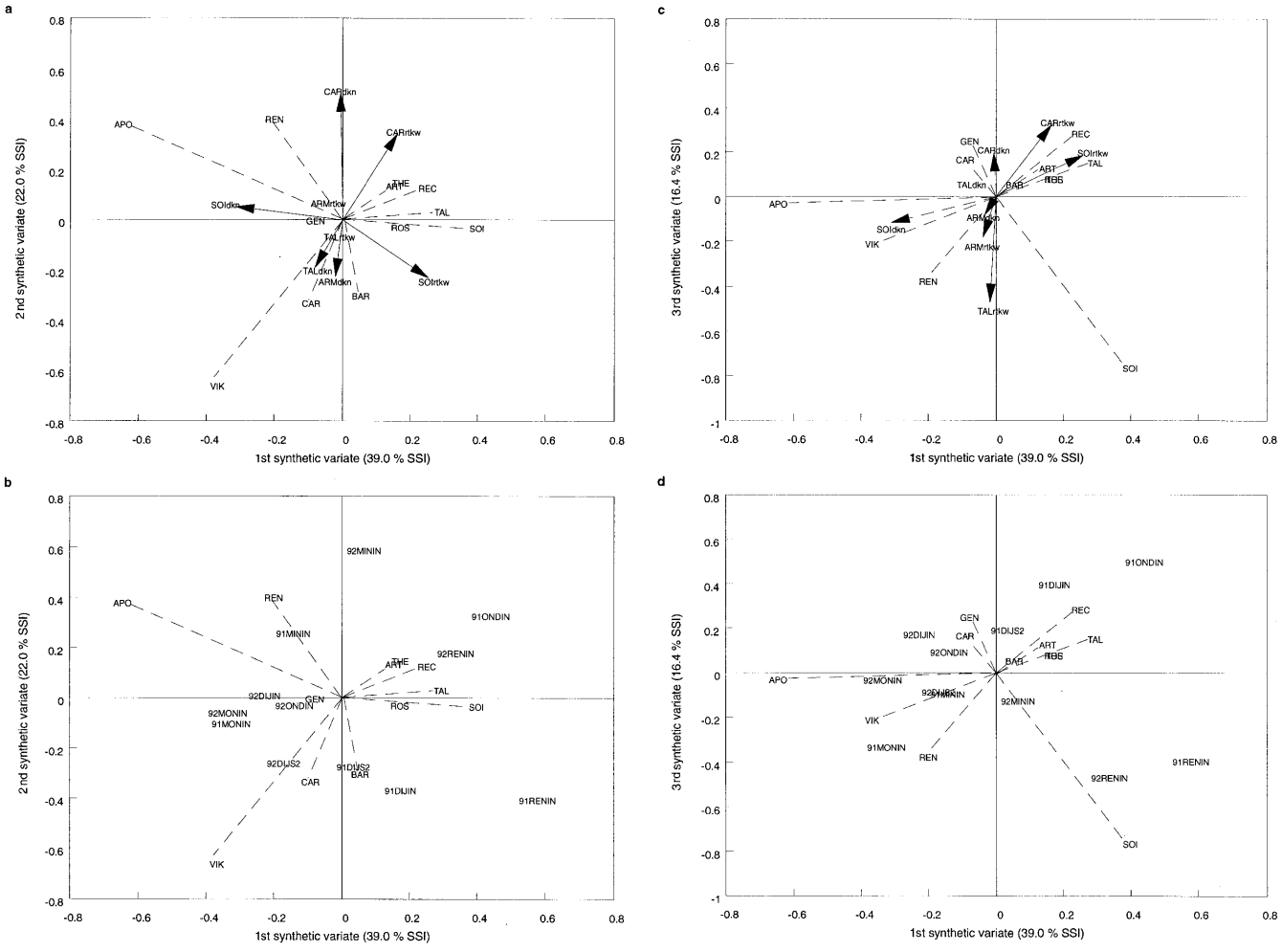

Fig. 3a–d Deviations of yield components measured on the probe genotypes as environmental covariates. Biadditive factorial regression biplots with 1st and 2nd synthetic variates (**a** and **b**) and 1st and 3rd synthetic variates (**c** and **d**). Parameters of genotypes (*dashed lines*) are displayed on all the plots while environmental covariates (*arrows*) are depicted in **a** and **c** and charaterizations of environments in **b** and **d**

near each other, such as 92MONIN and 91MONIN on one side and 91ONDIN and 92RENIN on the other. As for the genotypes, these patterns have to be confirmed with the analysis of the third term.

APO and REN showed positive interaction effects at 91MININ and 92MININ and negative interaction effects at 91RENIN and 91DIJIN. Best yields of VIK are obtained at 92DIJS2, 91DIJS2, 92MONIN and 91MONIN, while it yielded poorly at 92MININ, 91ONDIN and 92RENIN. SOI generally showed little interaction except at 91RENIN and 92RENIN (Fig. 3b).

The analysis of the genotype and environment parameters resulting from biadditive factorial regression helps to explain these particular behaviors (Fig. 3). Features from the two first axes are considered first (Fig. 3a and 3b). For SOIdkn, most of the environments are arranged from left to right with high SOIdkn (92MONIN, 91MONIN, 92DIJIN, 92ONDIN) to low SOIdkn (91RENIN). Considering SOIrtkw, 91MININ (low SOIrtkw) is opposite to 91RENIN (high SOIrtkw). For CARrtkw, 92DIJS2 and 91MONIN (low CARrtkw) are different from 91ONDIN (high CARrtkw).

An extra purpose of the biadditive factorial regression biplot is to give approximations about the coefficients for the factorial regression (van Eeuwijk et al. 1995). Projecting the genotype line on the concomitant variable arrows, it can be seen that APO, REN and VIK have the highest positive coefficients on SOIdkn, while SOI has the highest negative coefficient. In other words, when environments are unfavorable for the grain number formation of SOI (high SOIdkn), SOI behaved poorly while APO, REN and VIK behaved positively. One can assume that they could escape the poor conditions subjected to SOI during that period. Other conclusions can also be drawn: negative coefficients are observed for APO and REN with SOIrtkw. Thus APO and REN were probably not influenced by the same factors as SOI before flowering but were subjected to the same afterwards. VIK and CAR showed negative coefficients for CARrtkw while ART, THE and REC displayed positive ones. VIK, like CAR, behaved badly in unfavorable environments for CAR during the grain-filling period. Lastly, CAR also showed a negative coefficient with CARdkn.

Further information is given by the analysis of a third synthetic variate (Fig. 3c and d). On Fig. 3d, five of the six interactive environments can be considered but 92MININ, which is close to the origin, has to be ignored. For CARrtkw on this plot, the opposition between 91ONDIN (high) and 91MONIN (low) can be noted once again. The same opposition is found between them with SOIrtkw. Considering now TALrtkw, 91MONIN and 92RENIN (high TALrtkw) are opposite to 91DIJIN (low TALrtkw). Lastly, ARMrtkw was high at 92MININ and 92RENIN and low at 91DIJIN. APO, VIK and REN behaved especially well at 91MONIN. In this environment, the grain-filling period was favorable for genotypes like CAR or SOI and unfavorable for genotypes like TAL. Projecting the lines of the genotypes on the concomitant arrows of TALrtkw, these genotypes show positive coefficients for the factorial regression while those coefficients are negative for CARrtkw and SOIrtkw. They yielded better in good conditions during the grain-filling period for CAR or SOI, such as in 91MONIN, and yielded poorly in environments not favorable to CAR and SOI, such as in 91ONDIN.

On Fig. 3c, one can note once again the most interactive genotypes. Here SOI is quite different from REC, TAL, ART, ROS and THE. This was not revealed in Fig. 3a. The contrast between SOI and TAL, ART, ROS and THE can find an explanation with 92RENIN and 91DIJIN as these two environments are distinct for TALrtkw. The factorial regression coefficients of TAL, ART, ROS and THE are negative for TALrtkw but positive for SOI. TAL, ART, ROS and THE behaved in the same way at 91DIJIN (low TALrtkw) and 92RENIN (high TALrtkw): in the first they performed well during the grain-filling period but performed badly in the second. The behavior of SOI in these environments was opposite.

Usual indicators of yield-limiting factors as environmental covariates

To consider the usual indicators of yield-limiting factors as environmental covariates, a selection of variates is necessary because they are too numerous. This is done with a two-step approach where the traits DKN and

Table 5 Analysis of variance for DKN on the four probe genotypes. Interactive model (a). Partitioning of interaction with AMMI model (b) and biadditive factorial regression with all usual indicator(s) or after selection (d)

Interactive model

a

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	
Genotype (G)	3	1152.4	384.1	20.5	*
Environment (E)	11	5847.6	531.6	28.4	*
G*E	33	1420.0	43.0	2.3	*
Pure residual	36	674.7	18.7		

Partitioning of interaction

b

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*		Efficiency (% of SSI[a])
G*E	33	1420.0	43.0	2.3	*	100.0
1st term	13	733.9	56.5	3.0	*	51.7
2nd term	11	470.1	42.7	2.3	*	33.1
Remainder	9	216.0	24.0	1.3		

c

G*E	33	1420.0	43.0	2.3	*	100.0
1st term	10	704.2	70.4	3.8	*	49.6
2nd term	8	371.7	46.5	2.5	*	26.2
3rd term	6	100.2	16.7	0.9		
Remainder	9	243.9	27.1	1.4		

d

G*E	33	1420.0	43.0	2.3	*	100.0
1st term	8	630.3	78.8	4.2	*	44.4
2nd term	6	339.8	56.6	3.0	*	23.9
3rd term	4	62.0	15.5	0.8		
Remainder	15	387.9	25.9	1.4		

* Significant at the 0.05 probability level
[a] SSI: sum of squares of interaction

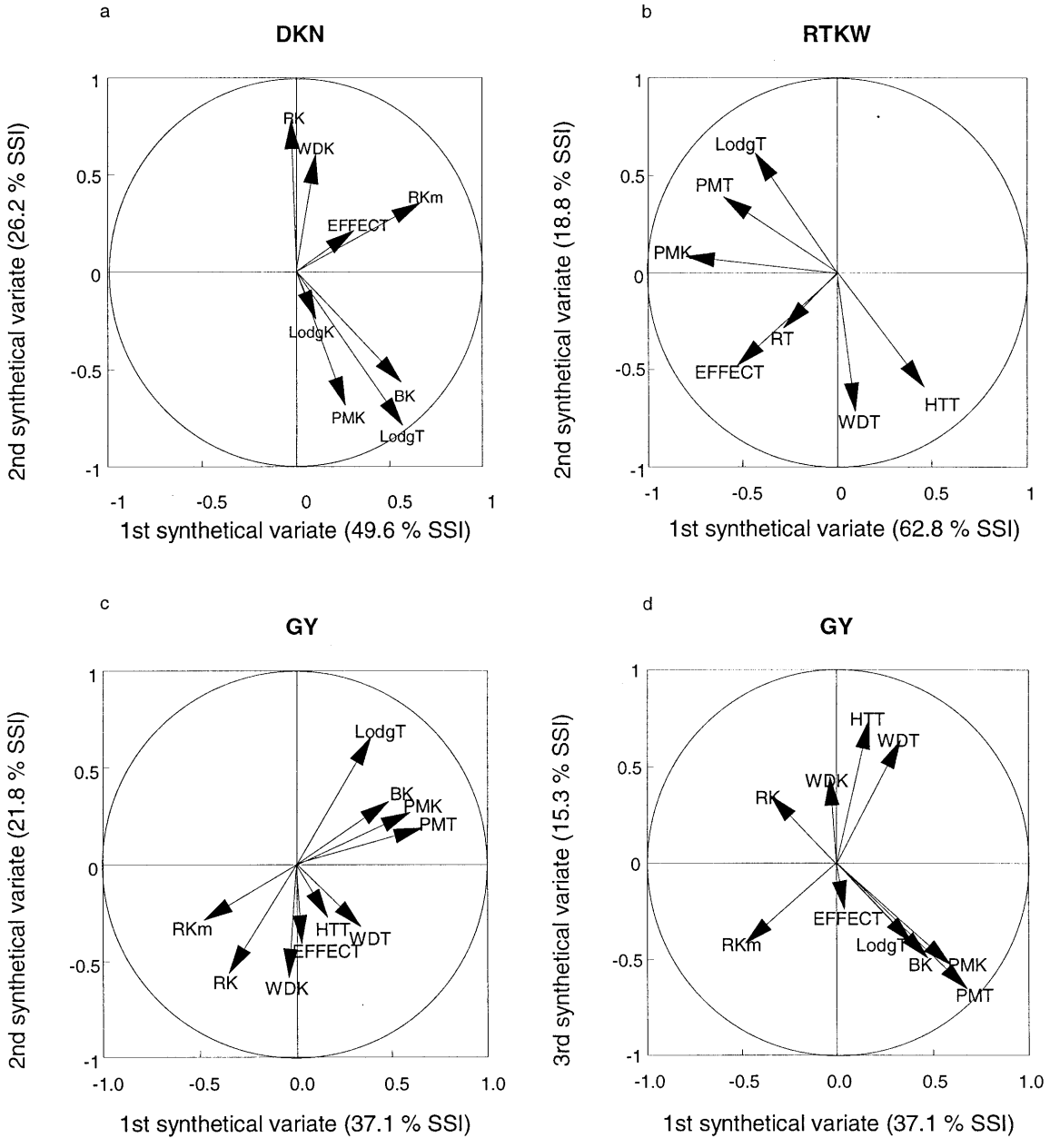

Fig. 4a–d Usual indicators of yield-limiting factors as environmental covariates. Contributions of each covariate to the synthetical environmental variates. Analysis of difference of kernel number (DKN) in (**a**), reduction of thousand-kernel weight (RTKW) in (**b**) and grain yield (GY) in (**c** and **d**). Analyses performed on the four probe genotypes for DKN and RTKW, and on the 12 genotypes for GY

RTKW are first analyzed to identify the useful environmental covariates for a further analysis of grain yield with the selected ones.

Difference of kernel number (DKN) in the four probe genotypes

As shown in Table 5a, genotype, environment and genotype*environment interaction were significant for the difference of kernel number (DKN) observed in the four probe genotypes. On average, DKN reached 7.8%; it varied from 0% (TAL) to 12% (ARM) between genotypes and from −18% to 20% between locations (Table 1). Differences were more extreme for combinations of genotype*environment: –31% (TAL at 91RENIN) to 31% (ARM at 92ONDIN). The classical biadditive model with two terms explained 84.8% of the interaction sum of squares using 72.7% of the degrees of freedom (Table 5b). Using a biadditive factorial regression with two or three terms, DKN was analyzed with eight environmental covariates (Table 5c): six variates directly related to grain-number formation (WDK, BK, RK, RKm, PMK and LodgK), the environmental main effect (EFFECT) and the level of lodging at maturity (LodgT). In cases of severe lodging during the grain-filling period (at 92MININ or 92RENIN for instance), kernel number could be underes-

timated due to kernel losses before or during harvest. This covariate was therefore added in the analysis of DKN. Most interaction (75.8 %) was explained with two terms (Table 5c); a third one was not significant.

Figure 4 gives some important clues about the contribution of environmental covariates to each of the multiplicative terms retained in the model. As in the multiple regression framework, it is difficult to directly interpret these regression coefficients due to possible colinearities between covariates. This is the reason why we recommend the interpretation from Fig. 4 which displays the correlations of the environmental covariates to the synthetic variates. Only the first and second synthetic variates are significant for DKN (Table 5c) and are considered in Fig. 4a.

Three major covariates contributed to the first term of DKN interaction: BK, RKm and LodgT (Fig. 4a). Five covariates contributed mainly to the second term: WDK, BK, RK, PMK and LodgT. On this second axis, WDK and RK were opposite to the three others. The best contributions were given by LodgT and, to a less extent, by WDK, BK and PMK. In addition, some covariates were common to both axes, such as LodgT and BK. LodgK, and the environmental main effect EFFECT, showed little contributions even for the third term.

Thus LodgK and EFFECT could be discarded from the initial set of environmental covariates. The corresponding results are given in Table 5d. A loss of efficiency, measured by the proportion of the sum of squares of the interaction (SSI) explained by the model, is observed for this selection, but this is compensated by an increase of parsimony.

Reduction of thousand-kernel weight (RTKW) in the four probe genotypes

The effects of genotype, environment and genotype*environment interaction were significant in the ANOVA for the reduction of thousand-kernel weight (RTKW) observed on the four probe genotypes (Table 6a). TKW was reduced up to 21.9% from its potential on average, the reduction varied from 19% (SOI) up to 25% (TAL) between genotypes, and from 12% (91MININ) to 31%

Table 6 Analysis of variance for RTKW on the four probe genotypes. Interactive model (a). Partitioning of interaction with AMMI model (b) and bi-additive factorial regression with all usual indicators (c) or after selection (d)

Interactive model

a

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	
Genotype (G)	3	311.6	103.9	21.4	*
Environment (E)	11	1279.2	116.3	24.0	*
G*E	33	1188.9	36.0	7.4	*
Pure residual	36	174.7	4.9		

Partitioning of interaction

b

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*		Efficiency (% of SSI[a])
G*E	33	1188.9	36.0	7.4	*	100.0
1st term	13	875.1	67.3	13.9	*	73.6
2nd term	11	244.2	22.2	4.6	*	20.5
Remainder	9	69.6	7.7	1.6		

c

G*E	33	1188.9	36.0	7.4	*	100.0
1st term	9	746.4	82.9	16.9	*	62.8
2nd term	7	223.4	31.9	6.5	*	18.8
3rd term	5	27.2	5.4	1.1		
Remainder	12	191.8	16.0	3.3	*	

d

G*E	33	1188.9	36.0	7.4	*	100.0
1st term	8	672.7	84.1	17.2	*	56.8
2nd term	6	196.9	32.8	6.7	*	16.6
3rd term	4	17.6	4.4	0.9		
Remainder	15	301.7	20.1	4.1	*	

* Significant at the 0.05 probability level

[a] SSI: sum of squares of interaction

(92RENIN) between environments. Great differences between genotype*environment combinations were also observed: 6% was recorded for SOI at 91MIN and 41% for TAL at 92RENIN (Table 1). AMMI models explained 94.1% of SSI at the cost of 72.7% of degrees of freedom with two terms (Table 6b). Seven covariates were introduced in biadditive factorial regression (Table 6c): five covariates directly related to the grain-filling period (WDT, RT, HTT, PMT and LodgT), the environmental effect (EFFECT) and the infection of powdery mildew before flowering (PMK). PMK was introduced because early infection of powdery mildew could affect TKW. This model with two terms explained 81.6% of SSI using 48.5 degrees of freedom. Higher values of efficiency were observed with three terms, but not significantly (respectively 83.9% and 63.6%).

With respect to RTKW, Fig. 4b gives an idea of the contributions of the environmental covariates to the two significant synthetic variates. The vector sizes are almost identical except for RT, indicating an equal contribution of each covariate. Nevertheless, the best contributions to the first term were given by PMK, whereas WDT, and to a lesser extent HTT, contributed more to the second one. Other covariates were related to both terms. As RT is poorly correlated to both axes ($|r| < 0.3$), we choose to discard it from the analysis. The corresponding information is given in Table 6d where 73.4% of SSI is partitioned by the model.

Grain yield (GY) in the 12 genotypes

All the selected environmental variates among the usual indicators related to DKN (initial ones except LodgK) and those related to RTKW (initial ones except RT) were introduced in a biadditive factorial regression model for the analysis of grain yield observed in the 12 genotypes. EFFECT was finally kept as it contributed to the explanation of RTKW (Fig. 4b). Two terms of the model explained 58.9% of the interaction with 31.4% degrees of freedom. Three terms partitioned 74.2% with 44.6% degrees of freedom (Table 3d).

For grain yield, three multiplicative terms were retained from the examination of Fig. 4c and d. Four covariates, all directly related to the grain-filling period – PMT, WDT, HTT, LodgT – stood out. All other covariates also contributed.

It is interesting to consider the interaction pattern of the 12 genotypes with respect to the ten selected environmental covariates (Fig. 5a and b). Dashed lines refer to genotypes and arrows to environmental covariates. Just as for the AMMI model, points (genotypes) near the origin display little interaction while points distant from it represent the most interactive genotypes; APO, VIK, SOI and REN being the most interactive. Points near each other (in both plots because three terms are significant in the model) display a similar interaction pattern, such as (ART, THE, TAL) or (ROS, BAR) for instance.

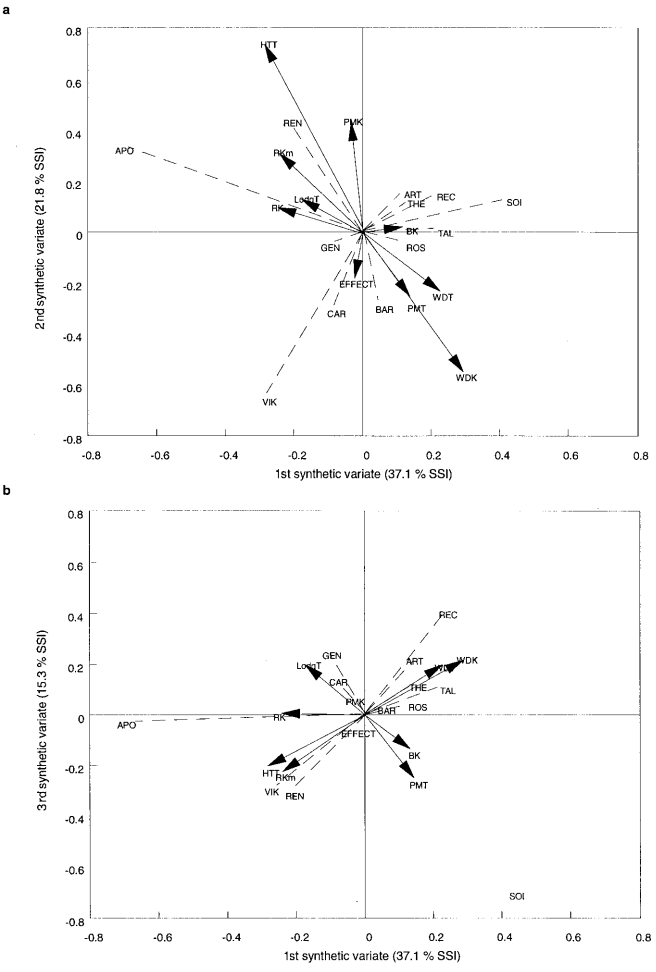

Fig. 5a, b Usual indicators of yield-limiting factors as environmental covariates. Analysis of grain yield performed on the 12 genotypes. Biadditive factorial regression biplots with parameters of genotypes (*dashed lines*) and coefficients of environmental covariates (*arrows*). 1st and 2nd synthetic variates are depicted in (**a**) and 1st and 3rd in (**b**)

Projecting the genotype dashed lines on the concomitant environment covariate arrows, it can be observed in Fig. 5a that REN has the highest positive coefficients on HTT, RKm or PMK, while its coefficient is negative on WDK, WDT or PMT. Thus, in comparison to the other genotypes of the experiment, its interaction is positive in hot environments during grain-filling or in environments with a high early pressure of powdery mildew. In contrast, its interaction pattern is negative in environments subject to water deficits (before or after flowering). APO gives positive coefficients on LodgT and RK, while ROS displays negative ones. The yield of APO increases with the duration of radiation. In comparison to others, it yielded better in environments subjected to lodging. The opposite is observed for ROS.

From Fig. 5b, it can be noted that there are positive coefficients for VIK and REN on HTT and RKm, but negative on WDK and WDT. For REN, a part of this information was already given in Fig. 5a. VIK and REN behaved similarly when subjected to water deficits or

high temperatures. REC, ART, THE and TAL behaved in the same way but are opposite to VIK and REN.

Discussion

Biadditive factorial regression models took into account an important component of the sum of squares from the genotype*environment interaction by means of linear functions of true measured environmental covariates, called ”synthetic covariates”. They revealed some important subsets of initial covariates related to the interaction. The use of contribution plots allowed more insight by interpreting the synthetic covariates from the initial environmental covariates. Applying a similar approach to Dutch maize variety trials, van Eeuwijk et al. (1995) also succeeded in identifying important environmental variates.

Van Eeuwijk et al. (1995) emphasized the power of biadditive factorial regression as it combines features of AMMI model and factorial regression, and thus provides useful information about the interaction. As for AMMI, the interactive pattern of the genotypes and the environments can be displayed in a biplot. In addition, the same biplot can provide a description of the environments with the environmental covariates, and the individual sensitivities of the genotypes can be also drawn. In comparison to the factorial regression model, which was also investigated (Brancourt-Hulmel 1999), biadditive factorial regression is more interesting because it took into account more information about the probe genotypes.

In this paper, the instability observed on grain yield can be related to deviations of yield components from potential values. These deviations, i. e. the difference of kernel number to the threshold (DKN) and the reduction of thousand-kernel weight from the potential (RTKW), are characteristics measured on probe genotypes and describe the environments during grain-number formation (DKN) and the grain-filling (RTKW). Introduced into a biadditive factorial regression as environmental covariates, they explained up to 77.4% of SSI with three terms (almost the same as AMMI) and helped to understand most of the genotype*environment interaction on the yield of a given set of genotypes.

The results obtained by Prihar and Stewart (1990) involving the use of a genetic harvest index for Sorghum, Corn and Wheat seemed to be promising for screening cultivars. But the authors did not show how instability of grain yield was related to it. In addition, it is impossible to determine when the stress occurs by observation of the harvest index since it corresponds to the whole plant cycle. By contrast, deviations of yield components from the potential allows one to determine the period involved, i.e. grain-number formation or the grain-filling period.

Dry matter biomass or other yield components could be observed, such as plant number per square meter and grain number per plant. But, obviously, further studies are needed to determine improved procedures for obtaining the potential values which represent basic data in such an approach. In this paper, they are obtained from experimental data. It would be interesting to investigate how crop models could help breeders to determine yield and yield-component potentials which seem to be essential in any study of genotype*environment interaction.

For introducing the usual indicators of yield-limiting factors in the model, which were too numerous, a two-step approach considering subsequently the analysis of the traits (DKN, RTKW) and grain yield was needed. Only the environmental covariates which affected DKN and RTKW in a first step were introduced in a second step into a biadditive factorial regression for the analysis of grain yield. The environmental variates were considered as poorly involved in the interaction of DKN and RTKW when the absolute value of their correlations with each synthetic covariate was below 0.3. An explanation of genotype*environment interaction for grain yield was more difficult since three multiplicative terms were needed. Most environmental covariates involved were related to the grain-filling period (PMT, WDT, HTT and LodgT). The contribution of the other covariates was less notable but the first analysis of DKN and RTKW showed that they had to be considered as well. This study clearly highlighted that crop diagnosis was very useful to determine covariates involved in genotype*environment interaction on grain yield. Based only on the analysis of grain yield, the results would have been less powerful.

The interest and application of an approach using biadditive factorial regression is to provide information about the interaction of the 12 genotypes with respect to the ten selected environmental covariates. In the same biadditive factorial regression biplot, the interaction pattern of the genotypes, as well as their sensitivities to environmental characteristics, can be given. Hence bi-additive factorial regression, which combines features of AMMI and factorial regression, gives detailed information about interaction.

In the present study, indicators of yield-limiting factors or deviations of yield components throw light on the genotype*environment interaction. Both descriptors might be of use to plant breeders. Sometimes, it can be easier to access probe genotypes; at other times, it is more interesting to use other descriptors. When the probe genotype is a well-known cultivar, for instance Soissons which is one of the most cultivated varieties in France at the present time, it can be obvious to compare a given genotype with it and conclude that this genotype could be cultivated in the same area as Soissons. It could thus simplify the advice to farmers who could adapt the mode of cultivation of Soissons to the newly released cultivar. In case of the specific adaptation of a genotype, the usual indicators of yield-limiting factors will be preferred. It could be indicated whether a genotype is sensitive to a given constraint (water deficits, high temperature) and thus locations subjected to the corresponding constraint could be discarded for its cultivation.

In applying this approach to variety trials or research programs,the standard design should be adapted by including probe genotypes of interest. Earliness is an important criterion for their choice but other traits could be added, such as sensitivities to nitrogen inputs or to the development of diseases. This depends on the program itself. For instance, in programs related to low-nitrogen-input agricultural systems, genotypes of extreme sensitivies to nitrogen deficiency could be introduced as probe genotypes in the experiment.

Concerning the traits measured in the probe genotypes, we preferred to incorporate covariates related to grain-number formation and to grain-filling instead of covariates defined for the whole-plant cycle in order to better capture events occurring before yield compensations. Nevertheless, it must be assumed that some bias could have been introduced because DKN and RTKW were observed only for the four probe genotypes. Another restriction was the manner used to determine the covariates. For instance, high temperature could be replaced by another criterion, the sum of degree days based on 28°C, and the results of ANOVA could be modified.

Since obtaining potential values for every genotype is not easy, analyzing a small set of genotypes gives a good compromise and the set of probe genotypes played a major role here in understanding what happened during the formation of yield. However, it might be objected that the interaction of the probe genotypes have to be well-representative of a given set of genotypes in order to be informative.

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