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ABSTRACT

Genotype × environment interaction is fully analyzed when genotypes and environments are well characterized. Probe genotypes were studied in a simplified crop diagnosis to show how variates of yield components can strengthen characterization of environments by usual indicators of yield-limiting factors. The objective of this study was to determine the main limiting factors of yield and to analyze their effects in wheat (*Triticum aestivum* L.) trials. Fixed genotypes (Talent, Soissons, Camp-Rémy, and Arminda) were studied as probe genotypes at five experimental stations of the Institut National de la Recherche Agronomique (I.N.R.A.) (Rennes, Mons, La Minière, Dijon, and Ondes) during 1991 and 1992. Two important variates, the reduction of kernel number and the reduction of thousand kernel weight, were analyzed to characterize the environments during the formation of yield. The former described the time-period until flowering and the latter the grain-filling period. In addition, factors that limit yield were determined through indicators such as water deficits, the ratio between nitrogen absorbed and kernel number, radiation, temperature, development of diseases (powdery mildew, strike rust, leaf rust, leaf and glume blotch), and lodging. Our study resulted in providing critical values for grain yield, kernel number, and thousand kernel weight for the four probe genotypes. Then reductions of yield components could be determined and analyzed. They provide useful information for characterizing environments subjected to numerous yield-limiting factors. Our study also revealed that the biological variates (essentially susceptibility to powdery mildew and to lodging) affected yield more than the climatic variates.

Explaining genotype × environment interaction is central in a wheat breeding program. Under French conditions, environmental effects are very often greater than genotypic effects in multi-environment trials. Thus environments have to be well characterized to explain genotype × environment interaction. What is the best method to characterize environments? Factors that limit yield can be identified a posteriori by a crop diagnosis (Sebillotte, 1980; Doré et al., 1997). When yield, compared with a preestablished optimal value, is reduced, one or several factors limited yield. The winter wheat cycle is quite long (8–11 mo. in France), during which numerous factors can impinge upon expression of yield. The relationship between the two main yield components, kernel number per square meter (KN) and thousand kernel weight (TKW), can be helpful for diagnosing yield-limiting factors. Below the KN threshold, there is no competition for assimilates between kernels, and TKW can be maximal. Above the KN threshold, TKW decreases as KN increases according to an hyperbolic relationship. Applying this to winter wheat, Leterme et al. (1994) fully described how to interpret this relationship between TKW and KN.

Because these two yield components are developed over two distinct crop development periods, (from sowing to flowering for KN and after flowering for TKW), this allows identification of when the limiting factors occur. Their intensity is determined by comparison to reference values considered as threshold or potential values. Additionally, to discover which factors or conditions are responsible for yield reductions, it is necessary to characterize the nutritional status of the crop and the environmental and biological constraints and relate these indicators to yield component reductions. These factors are numerous in winter wheat trials. Climatic constraints include water deficits (Singh, 1981; Kobata et al., 1992; Debaeke et al., 1996), temperature (Wiegang and Cuellar, 1981; Hunt et al., 1991; Stone and Nicolas, 1995a, b), and radiation (Demotes-Mainard et al., 1996). In French cropping systems, biological constraints are associated with diseases. More than 20 diseases of major significance have been reported on wheat (McIntosh, 1998). The effect of diseases on yield depends on many factors including the nature of the disease, its intensity, its distribution, its duration, the susceptibility of the genotype, the stage of the plant when infection occurs, and the method of estimation. Analysis in trials requires investigation of the interaction between several diseases. The interaction of several diseases is also an important consideration as shown by Chevalier-Gérard et al. (1994) who found that stripe rust (*Puccinia striiformis* West.), septorias (*Septoria tritici* Rob. in Desm. and *Stagonospora nodorum* (Berk.) Cast. & Germ.), and powdery mildew (*Erysiphe graminis* DC f. sp. tritici) had the greatest effect on yield loss in northern France from 1978 to 1991. In wheat, crop diagnosis was applied to wheat on-farm field trials by Meynard et al. (1981), Meynard and David (1992) and Leterme et al. (1994). The method has also been adapted to series of variety trials by Lecomte (1994) for wheat and by

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Abbreviations: BK, ratio between nitrogen absorbed during the whole cycle and kernel number; E, environment; ETa, actual evapotranspiration; ETm, maximal evapotranspiration; −F, medium sowing date without fungicides; G, genotype; GY, grain yield; HTT, high temperature during grain-filling; IN, medium sowing date with fungicides; KN, kernel number per square meter; L, location; LodgT, lodging during grain-filling; LGBT, leaf and glume blotch during grain-filling; LRT, leaf rust during grain-filling; PMK, powdery mildew during grain number formation; PMT, powdery mildew during grain-filling; RGY, reduction of grain yield; RK, radiation during grain number formation; RKm, radiation ± days at meiosis; RKN, reduction of kernel number; RT, radiation during grain-filling; RTKW, reduction of thousand kernel weight; S2, late sowing date with fungicides; TKW, thousand kernel weight; T, treatment; WDK, water deficits during grain number formation; WDT, water deficits during grain-filling; Y, year.

Desclaux (1996) for soybean. These analyses identified limiting factors of yield with their respective intensities.

Winter wheat field trials were conducted during 2 yr (1991–1992) in France at five locations of the Institut National de la Recherche Agronomique (I.N.R.A.) to show how probe genotypes can strengthen a characterization of environments by usual indicators of yield-limiting factors. These data should help define relationships between yield component losses observed in probe genotypes and indicators of yield-limiting factors such that environments in wheat trials can be characterized. Three steps were required for this approach: (i) determination of reference values of yield components for each probe genotype, (ii) determination of the reductions of yield components from the reference values and (iii) analysis of the reductions of components with respect to yield-limiting factors. Such information is important for further investigation of genotype × environment interaction.

MATERIALS AND METHODS

Probe Genotypes

In multi-environment trials, genotypes often differ for earliness. Thus, it is doubtful that all genotypes are submitted to the same limiting factors. Observation of yield formation of a single genotype is not sufficient and it is necessary to observe several genotypes that vary in earliness to cover the broadest development cycle possible. Hence, four genotypes were used for crop diagnosis and will be termed as probe genotypes: Talent, Soissons, Camp-Rémy, and Arminda. On a scale of earliness at heading from 1 (very late) to 9 (very early), Arminda scores 4.5, Camp-Rémy 6, Soissons 7, and Talent 7.5 (GEVES, 1992). On average, Arminda flowered 12 d after Talent during the experiment. Soissons was the most resistant to lodging and to powdery mildew before flowering, but the most susceptible to leaf rust during grain filling. Thus, probe genotypes defined here were a specific set of fixed genotypes selected for their known response to several environmental factors occurring in the trials. The concept was similar to what Cooper and Fox (1996) considered as probe genotypes.

Determination of Reference Values for Grain Yield, Kernel Number, and Thousand Kernel Weight of Probe Genotypes

A long-term experiment with these probe genotypes has been carried out since 1987 (Lecomte, 1994) in different locations of the INRA network. To complete the database for yield components of these genotypes, data have also been collected from the ITCF (Institut Technique des Céréales et des Fourrages) network (Gate, 1995, 1998, personal communication) and from other INRA studies (Oury, 1990, 1993; Robert, 1996; Trottet, 1998; Le Gouis, 1998, personal communication). Reference values for grain yield are determined by the maximal value of the database for each probe genotype. As shown by Leterme et al. (1994), the relationship of KN to TKW shows a boundary line (Webb, 1972), beyond which the data do not extend. This boundary line is characterized by three parameters (Fig. 1): potential TKW, which is the maximum value of TKW, only reached when KN is low; KN threshold, beyond which the boundary TKW decreases; and grain yield, which reaches its maximum value at KN × boundary TKW. Maximal TKW and KN threshold were determined by resampling to estimate variability. For each probe genotype, 1000 samples containing 10% of the total number of observations were obtained by a simple random sampling with replacement. Maximum TKW and KN threshold values were determined for each sample. A confidence interval was estimated from the 1000 values.

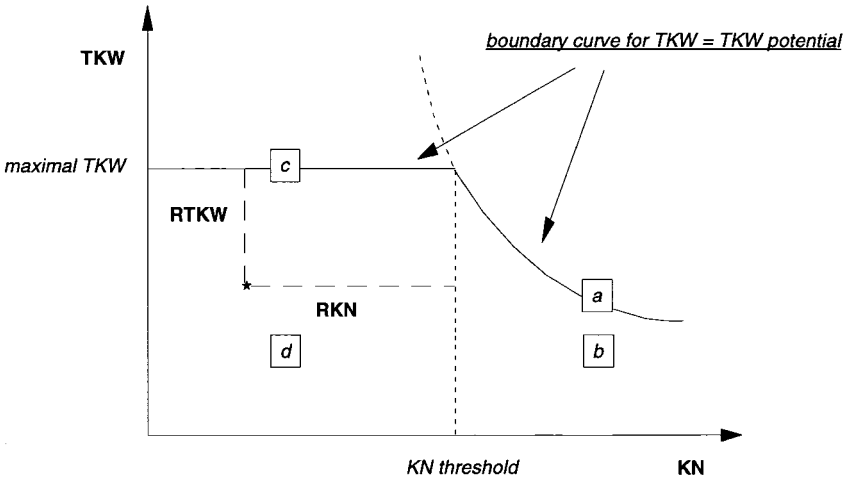

Fig. 1. Principle of crop diagnosis and estimation of reductions of yield components (adapted from Leterme et al., 1994): reduction of kernel number (RKN) & reduction of thousand kernel weight (RTKW).

Determination of Reductions of Kernel Number (RKN) and Thousand Kernel Weight (RTKW)

Two variates or outputs were calculated from the theoretical function of TKW with respect to KN for each probe genotype in each environment (Fig. 1). The reduction of kernel number was defined by RKN = max[0;100 × (KNthreshold − KN)/KNthreshold]. This value characterized the grain number formation. Reduction of kernel number can vary from 0 (no damage) to 100 (heavy damage). When KN ≥ KNthreshold, RKN was equal to zero and indicated that yield was not limited by the grain number formation. The reduction of thousand kernel weight was defined by RTKW = max[0;100 × (potentialTKW − TKW)/potentialTKW] and described the grain-filling period. Environments were considered as optimal for this period when TKW of each probe was equal to the potential value, and suboptimal when the component was reduced. Potential TKW corresponded to the maximal TKW when KN < KNthreshold and was given by the hyperbolic relationship between TKW and KN when KN > KNthreshold. When due to experimental error, observed TKW is higher than potential TKW, RTKW is forced to zero. These reduction values are outputs of crop diagnosis and can be used as environmental variables for characterizing the environment for further investigation of the genotype × environment interaction. A similar criterion was also determined for grain yield (RGY).

Indicators for Yield-Limiting Factors

Several variables were used as indicators for yield-limiting factors. Indicators for the period of grain number formation were identified by K (for Kernel number) while those for the grain filling were symbolized by T (for Thousand kernel weight) in last position of the codes. The first period was concerned with the cumulative water deficits from beginning of stem elongation to flowering (WDK). WDK is the daily difference between maximal evapotranspiration, ETm, and actual evapotranspiration, ETa. ETa is deduced from the potential evapotranspiration according to the relationship ETa = $kc \times ks \times$ ETp, where *kc* is a coefficient which varies with the stage of the crop and *ks* a coefficient which varies with the root-zone water content (Gate, 1995). When root-zone water content is sufficient, ETa = ETm = $kc \times$ ETp (Gate, 1995). ETp, determined from the Penman equation, was provided by national or INRA weather stations of each site. The ratio between nitrogen absorbed during the whole cycle and kernel number (BK) was used to indicate nitrogen stress during the crop cycle, mainly during the formation of grain number (Meynard et al., 1981; Meynard, 1987). The sum of daily radiation from beginning of stem elongation to flowering (RK), the sum of daily radiation ± 3 d at meiosis (RKm), and powdery mildew (PMK), were also observed. During that period, no lodging nor days with minimum daily temperature below −4°C were observed. For the grain-filling period, the sum of water deficits (WDT), the sum of daily radiation (RT), and high temperature estimated by the sum of degree days based on 25°C (HTT) were also computed. Powdery mildew (PMT), leaf rust (LRT), and leaf and glume blotch (LGBT) were observed. No stripe rust was noticed in the network during 1991 and 1992. Development of diseases were observed on the probe genotypes and corresponded to the maximum scores noted on a given probe genotype. Other indicators were calculated according to the cycle of each probe genotype and climatic data were provided by the nearest standard meteorological station in each trial. Mean and range of yield-limiting factors are given in Table 1.

Description of Trials

Field trials were conducted during 2 yr (1991–1992) in France at five locations of the I.N.R.A. winter wheat breeding network: Mons (49°56′N Lat., 2°56′ E Long.), La Minière (48°48′ N, 2°08′ E), Rennes (48°05′ N, 1°41′ W), Dijon (47°19′ N, 5°01′ E), and Ondes (43°36′ N, 1°26′ E). At each site, the design was a randomized complete block. Plot size varied between locations from 5.9 (Rennes) to 7.8 m^2 (La Minière). Overall, two blocks were conducted except at Mons in 1992, where the experiment was conducted with three blocks. Two agronomic treatments were applied: medium-late sowing date at Dijon, treatment with and without fungicides at La Minière, Mons, Rennes and Ondes. Agronomically, each site was treated according to its individual requirements with respect to nitrogen uptake, pest infestation, plant density, and weed competition. At the end of winter, plant densities were all above 300 plants/m^2. At Dijon, the two treatments received fungicides. For the analysis of genotype × environment inter-

Table 1. Mean and range of yield-limiting factors for kernel number formation and grain filling period from the 20 environments. Scale for diseases and lodging: 1 = low to 9 = high development.

Yield-limiting factors		Symbol	Unit	Mean	Std	Min	Max
Kernel number formation							
Climatic variates							
water deficit	Σ(ETm − ETa) from begin. stem elong. to flowering	EDK	mm	7.0	14.3	0.0	54.0
temperature	number of days with min daily temp <−4°C			no frost			
radiation	radiation days ±3 days at meiosis	RKm	MJ/m^2	14.2	2.7	8.2	17.8
	radiation days from ear at 1 cm to flowering	RK	MJ/m^2	111.5	11.3	93.7	133.9
Diseases							
powdery mildew		PMK	score	1.6	1.3	1.0	5.1
Lodging				no lodging			
Nitrogen status	coefficient BK	BK	mg/grain	1.27	0.13	1.00	1.47
Grain filling period							
Climatic variates							
water deficit	S(ETm − ETa) from flowering to maturity	WDT	mm	16.4	21.0	0.0	72.7
high temperature	degree days from flowering to maturity based on 25°C	HTT	°C	26.6	13.2	10.1	55.9
radiation	radiation days from flowering to maturity	RT	MJ/m^2	68.0	4.5	58.1	74.9
Diseases							
powdery mildew		PMT	score	1.6	1.2	1.0	5.1
stripe rust				no infection			
leaf rust		LRT	score	1.3	0.7	1.0	3.8
leaf and glume blotch		LGBT	score	1.5	1.4	1.0	5.8
Lodging		LodgT	score	2.7	2.1	1.0	7.0

action, each combination of year × location × treatment was considered as one environment and a total of 20 environments were investigated. Each environment was identified by the year (1991 or 1992), by the location (DIJ, MIN, MON, OND and REN), and by the treatment (IN for medium sowing date with fungicides, −F for medium sowing date without fungicides and S2 for late sowing date).

The four genotypes were studied in all the environments except at Ondes where Arminda was missing during the 2 yr. The values for Arminda have been estimated by Apollo, a genotype of the same earliness; a preliminary study from 36 environments of the total database revealed very high correlations for RKN and RTKW between the two genotypes (0.94 and 0.92, respectively).

Plant Sampling and Measurements

In most environments, each genotype was sown on two adjacent plots. Grain yields were determined by mechanically harvesting all six rows of one of the two plots at maturity, and disease susceptibility, height, and lodging susceptibility were also observed. About 1 d before mechanical harvest, 150 shoots were cut at ground level in the same plot in the inside four rows in order to determine yield components. In each experimental plot, the kernel number per square meter (KN) was deduced from the relationship GY = KN × TKW. In the remaining plot, plants were sampled at the beginning of stem elongation (precisely when the distance between the base of the first leaf and the top of the young ear reached 10 mm) to determine the vegetative biomass production at this stage, nitrogen content, and density of plants. At Mons, there was a third plot specific to yield component measurements.

Statistical Developments

The statistical analyses, correlations, principal component analyses (PCA) and conventional analyses of variance, were all performed by SAS Software System (1989). Biadditive analyses and corresponding plots were carried out by the INTERA package on a PC (Decoux and Denis, 1991). Effects were evaluated according to the following model of analysis of variance:

$$E[Y_{gek}] = \mu + \alpha_g + \beta_e + b_{ek} + \alpha\beta_{ge},$$

where $E[Y_{gek}]$ is the expectation of a given observation Y_{gek} for Genotype g grown in Block k in Environment e, μ is the grand mean, α_g is the genotype main effect, β_e is the environment main effect, b_{ek} is the effect of block k in Environment e and $\alpha\beta_{ge}$ is the interaction between genotype and environment. All terms were considered as fixed effects. In addition, the environment effect was partitioned into year, location, treatment and the corresponding interaction terms. The partitioning was applied to environment main effect β_e as well as to the interaction term $\alpha\beta_{ge}$. Ecovalences (von Wricke, 1962) were computed for each probe Genotype g, $W_g^2 = \Sigma_{e=1}^{20} (Y_{ge} - Y_{g.} - Y_{.e} + Y_{..})^2$, where Y_{ge} is the mean of genotype g grown in Environment e, $Y_{g.}$ is the mean of genotype g, $Y_{.e}$ is the mean of Environment e and $Y_{..}$ the grand mean. They were expressed as a percentage of the total interaction. In addition, interaction was also modeled with a multiplicative model (Mandel, 1971) also called AMMI (Gauch, 1992) with two multiplicative terms to characterize and illustrate the contrasted behavior of the genotypes by parameters. This model is written as follows:

$$E[Y_{ge}] = \mu + \alpha_g + \beta_e + \lambda_1\gamma_{g1}\delta_{e1} + \lambda_2\gamma_{g2}\delta_{e2}$$

where λ_1 is the singular value which accounts for the interaction part explained by the first term, γ_{g1} is the normalized genotype vector describing genotype differences, and δ_{e1}, similarly for the environments; λ_2, γ_{g2}, and δ_{e2} are assigned to the second term involving orthogonality constraints with the first term. Other terms of the model, $\mu + \alpha_g + \beta_e$, correspond to the additive part.

Correlation matrix containing yield components reductions of each probe genotype and indicators of yield-limiting factors were analyzed according to Principal Component Analysis (PCA). Interpretation of the correlation matrix was guided by the analysis of a plot displaying correlations between each variate to each component in Cartesian diagrams. Because the analysis was done on the correlation matrix, the component loadings are standardized component loadings and the magnitude and sign of the loadings essentially reflect the correlation of the variate to the component. Variates with loadings around

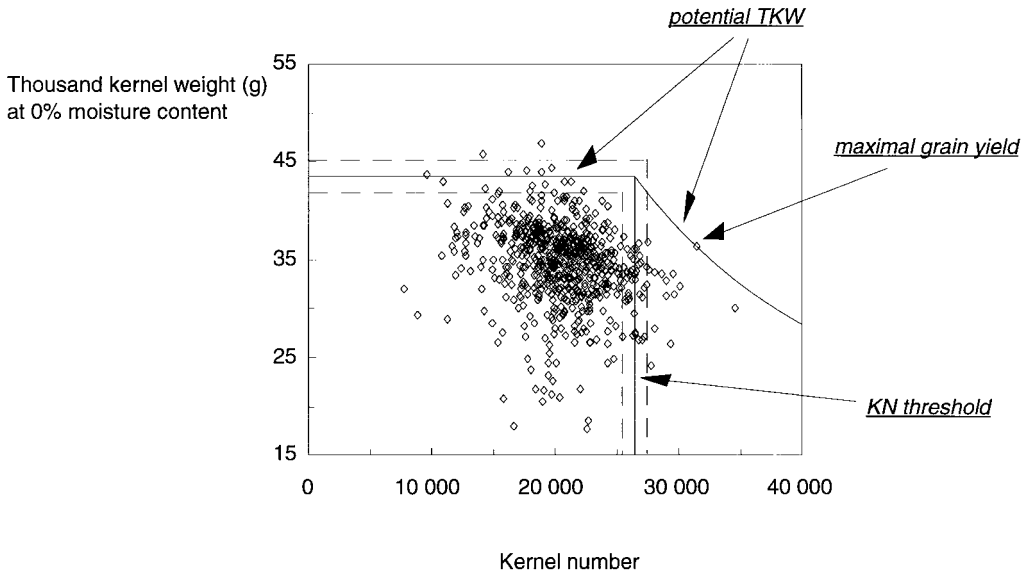

Fig. 2. Boundary curve and thresholds for kernel number (KN) and thousand kernel weight (TKW) determined for Soissons. Data collected from INRA (Hulmel, Lecomte, Le Gouis, Meynard, Oury, Robert, Trottet) and ITCF (Bernicot, Gate). Confidence intervals of thresholds obtained by resampling are symbolized in dashed lines.

0 are not correlated to the component. The sign of the standardized loading indicates whether the variate is positively or negatively correlated to what the component is summarizing.

RESULTS AND DISCUSSION

Determination of Reference Values of Yield Components for Each Probe Genotype

Reference values of yield components were determined by a single boundary curve, common to all the environments in order to make fair comparisons between them in a multi-environment experiment. Data collected for Soissons are illustrated in Fig. 2 where references values for kernel number and thousand kernel weight are noted with a solid line and the corresponding confidence intervals are noted with dashed lines. The solid line corresponds to the boundary curve describing the relationship between thousand kernel weight and kernel number. Table 2 shows that the reference values differ between the probe genotypes. Talent shows the highest thousand kernel weight (45.1 g) while Camp-Rémy obtains the lowest one (41.8 g). The highest threshold of kernel number is displayed by Soissons (26464/m^2) and the lowest one by Talent (22781/m^2).

Determination and Analysis of the Reductions of Yield Components

Reductions of yield components (RKN and RTKW) from the previous references values can estimate in intensity the action of yield-limiting factors. They were determined for the four probe genotypes in the 20 environments (Table 3). Analysis of variance showed that reduction of kernel number (RKN), and reduction of thousand kernel weight (RTKW), as well as grain yield (GY) were affected by genotype, environment, and genotype × environment interaction effects (Table 4). The environmental effect was important since all components including the different interaction terms between year, location, and treatment were significant. The genotype × environment interaction was mainly due to genotype × location and genotype × year × location effects for grain yield and RKN. For RTKW, the genotype × treatment interaction was the single nonsignificant effect. On average, reduction was greater for thousand kernel weight (24%) than for kernel number (8%) but this was different between genotypes and environments (Table 3). Some differences were observed between environments. Grain number reduction varied from 0 to 24 and only five environments (91MININ, 91RENIN, 91REN−F, 91MIN−F, and 91DIJIN) displayed low RKN (respectively, 0, 0, 2, 3, and 4). The highest reduction of KN was recorded at 92OND−F. Thousand kernel weight was more affected and varied from 12% (91MININ) to 39% (92REN−F).

Table 2. Potential values for the four probe genotypes. Std = standard deviation.

Genotype	Number of observations	Maximal yield	Maximal TKW ± std	KN threshold ± std
		Mg/ha 0% moist. cont.	g 0% moist. cont.	m^{-2}
Arminda	412	10.7	43.0 ± 1.46	24 737 ± 855
Camp-Rémy	335	10.2	41.8 ± 1.43	24 414 ± 811
Soissons	699	11.5	43.4 ± 1.70	26 464 ± 1025
Talent	488	10.2	45.1 ± 3.49	22 781 ± 1864

The correlations between grain yield and reductions of yield component are given in Table 5. Grain yield was negatively correlated to RKN ($r = -0.63$) and RTKW ($r = -0.71$) indicating a similar impact on grain yield formation. No correlation was found between RKN and RTKW. This important result was helpful for determining yield-limiting factors as it suggested that there were probably independent factors between each period of yield formation, grain number formation, and grain filling.

Hence, yield was affected during the grain number formation as well as the grain-filling period and some differences were observed between environments. The best yield observed at 91MININ was related to good conditions during the formation of yield, particularly during the formation of grain number. 92REN−F yielded poorly and this was associated to both periods of the formation of yield, particularly during grain filling. 92MONIN and 91REN−F yielded the same but in a quite different way: with a high reduction of thousand kernel weight for 91REN−F and with moderate reductions of both components for 92MONIN. This reveals that the evaluation of the reduction of yield components is helpful to further understand how yield was limited.

Furthermore, contribution for each probe genotype to interaction, measured by the ecovalence, was different for GY, RKN, and RTKW. Camp-Rémy was slightly interactive for GY (low ecovalence of 8.7%) in comparison to the three others (high ecovalences of 24.9, 27.7, and 38.7%). In contrast, Camp-Rémy was nearly the most interactive during the grain-filling period (30.3% for RKN) and was equivalent to Soissons and Talent during the grain number formation (respectively 29.8, 31.9, and 30.2% for RTKW). The interaction pattern, when a multiplicative model with two terms is applied, is given for the four probe genotypes in Fig. 3. For grain yield, Camp-Rémy (CAR) was near the origin indicating little interaction (low multiplicative parameters on both axes) while the three others [Arminda (AMR), Soissons (SOI), and Talent (TAL)] were more distant from each other. With respect to reduction of kernel number, all genotypes displayed different interaction patterns, Camp-Rémy, and Talent being the most interactive. About reduction of thousand kernel weight, Soissons was less interactive than the others, which were distant from the origin and distant one from each other, indicating distinct interaction pattern.

Camp-Rémy is a probe of interest because it shows an interaction pattern very different among GY, RKN, and RTKW. This particular behavior suggests that the analysis of yield reductions could be complementary to the analysis of grain yield. In addition, the four genotypes are all important to consider as they display diverse interaction pattern for grain yield, and for the reductions of yield components. What could be observed with fewer probe genotypes?

Analysis of the Reductions of Components with Respect to Yield-limiting Factors

Correlations between variates associated with the grain number formation are analyzed according to a

Principal Component Analysis (Fig. 4). The first component captures 37% of the variation in the correlation matrix. In the plot of the variates (top plot), this component indicates that as reductions of kernel number for Arminda (ARMrkn, loading ~+0.85), Soissons (SOIrkn), Camp-Rémy (CARrkn), and Talent (TALrkn, loading ~+0.35) increase, GY (loading ~−0.75), radiation (RK), water deficits (WDK), nitrogen status (BK), and radiation at meiosis (Rkm, loading ~−0.35) decrease. Loading of powdery mildew (PMK) is near 0 (not related to this component). The component is describing the variation related to the association between variates of reductions (RKNs) and the GY, RK, and BK variates.

The plot of the individuals (i.e., environments) along this first component (bottom plot) orders 91REN, 91MIN, and 91DIJ on the left to 92REN, 92DIJ, 92MIN, and 91MON and 92MON in the middle to 91ONDIN and 92ONDIN on the right. Generally treatments (IN, −F, or S2) for a location do not show a large separation on this component, at least relative to the separation of sites and in some cases different years for a site. The component gradient is higher yield, lower RKNs at −3 loading to lower yield, higher reductions of kernel number at +3.

Best yields were mostly obtained for higher values of radiation. In such conditions, most of the probe genotypes (Arminda, Soissons, and Camp-Rémy) showed little reductions of kernel number. Talent had a particular behavior which could be analyzed on the second component.

The second component is 25% of the variation in the correlation matrix. This component indicates that as PMK (loading ~+0.8), BK, TALrkn, and CARrkn

Table 3. Main features of the environments during the formation of grain number and the grain-filling period. Means of 4 probe genotypes excepting for individual reductions of yield component. Definition of symbols is given in Table 2. In addition, TALrkn, SOlrkn, CARrkn, and ARMrkn stand for reduction of kernel number, respectively for Talent, Soissons, Camp-Rémy and Arminda. TALrtkw, SOlrtkw, CARrtkw, and ARMrtkw stand for reduction of thousand kernel weight, respectively for Talent, Soissons, Camp-Rémy and Arminda. 91 and 92 code for year, DIJ, MIN, MON, OND, and REN code for respectively Dijon, Minière, Mons, Ondes, and Rennes. IN, −F, and S2 code for treatments, respectively standard, without fungicides, and late sowing date.

					Formation of grain number							
Environments	GY	RGY	RKN	TAL rkn	SOl rkn	CAR rkn	ARM rkn	WDK	BK	RK	RKm	PMK score
	Mg/ha	%						mm	mg/grain	MJ/m²		
91DIJIN	8.3	22	4	5	4	4	4	42.1	1.3	133.9	14.8	1.0
91DIJS2	7.6	29	9	4	12	6	15	46.6	1.3	129.1	16.2	1.0
92DIJIN	7.5	29	13	2	14	16	19	20.8	1.1	112.7	16.0	1.0
92DIJS2	7.8	27	8	4	10	11	11	21.6	1.2	104.2	17.8	1.0
91MIN-F	7.4	31	3	0	2	7	8	0.0	1.3	115.4	14.1	1.0
91MININ	9.3	13	0	0	0	1	0	0.0	1.3	115.4	14.1	1.0
92MIN-F	6.1	43	16	7	14	20	24	0.0	1.4	98.0	16.2	1.0
92MININ	6.8	36	12	3	6	29	13	0.0	1.4	98.0	16.2	1.0
91MON-F	5.7	46	20	13	17	30	20	0.0	1.3	124.8	14.2	1.0
91MONIN	7.5	30	12	1	15	19	14	0.0	1.4	124.8	14.2	1.0
92MON-F	6.4	40	16	5	25	16	16	0.0	1.1	112.8	17.5	1.0
92MONIN	6.7	37	18	14	23	16	18	0.0	1.1	112.8	17.5	1.0
91OND-F	5.8	44	17	3	17	31	30	0.0	1.2	114.3	8.2	1.0
91ONDIN	6.2	42	17	0	23	14	28	0.0	1.2	114.3	8.2	1.0
92OND-F	6.2	42	24	7	28	26	36	4.9	1.0	93.7	11.9	1.0
92ONDIN	6.5	39	21	6	23	23	31	4.9	1.1	93.7	11.9	1.0
91REN-F	6.7	37	2	0	0	5	4	0.0	1.4	113.2	13.3	2.4
91RENIN	8.7	18	0	0	0	0	0	0.0	1.4	113.2	13.3	2.8
92REN-F	5.3	51	20	18	13	29	19	0.0	1.5	103.0	14.5	4.8
92RENIN	6.5	39	13	12	4	18	14	0.0	1.5	103.0	14.5	5.1

					Grain filling period									
Environments	GY	RGY	RTKW	TAL rtkw	SOI rtkw	CAR rtkw	ARM rtkw	WDT	HTT	RT	LodgT score	PMT score	LRT score	LGBT score
	Mg/ha	%						mm	°C	MJ/m²				
91DIJIN	8.3	22	19	17	19	19	19	68.1	51.9	74.9	1.0	1.0	1.0	1.0
91DIJS2	7.6	29	22	23	20	23	20	68.7	55.9	72.9	1.0	1.0	1.0	1.0
92DIJIN	7.5	29	18	24	17	20	14	1.5	28.1	69.3	1.4	1.0	1.0	1.0
92DIJS2	7.8	27	20	23	18	16	23	0.7	24.3	68.3	1.5	1.0	1.0	1.0
91MIN-F	7.4	31	28	34	20	23	35	22.0	27.1	66.3	3.9	5.1	1.0	1.0
91MININ	9.3	13	12	11	6	13	19	22.0	27.1	66.3	2.8	2.0	1.0	1.0
92MIN-F	6.1	43	32	35	27	28	38	5.2	15.2	65.7	7.0	4.8	2.6	1.0
92MININ	6.8	36	27	29	22	19	37	5.2	15.2	65.7	6.8	2.0	1.0	1.0
91MON-F	5.7	46	33	42	33	22	33	2.3	20.5	66.3	1.5	3.0	1.0	1.0
91MONIN	7.5	30	20	27	18	13	20	2.3	20.5	66.3	1.0	1.0	1.0	1.0
92MON-F	6.4	40	28	31	25	29	30	0.0	10.1	73.0	1.8	1.5	1.0	5.5
92MONIN	6.7	37	24	29	20	22	23	0.0	10.1	73.0	1.0	1.3	1.0	5.8
91OND-F	5.8	44	31	38	33	31	18	31.2	42.1	69.2	1.0	1.1	1.0	1.0
91ONDIN	6.2	42	30	33	27	36	24	31.2	42.1	69.2	1.0	1.1	1.0	1.0
92OND-F	6.2	42	22	31	21	28	10	13.7	34.1	58.1	1.6	1.0	1.0	1.0
92ONDIN	6.5	39	22	36	21	24	7	13.7	34.1	58.1	2.1	1.0	1.0	1.0
91REN-F	6.7	37	36	27	32	33	48	16.1	14.9	66.6	2.6	1.0	1.5	1.0
91RENIN	8.7	18	19	15	15	13	30	16.1	14.9	66.6	2.0	1.0	1.5	1.0
92REN-F	5.3	51	39	41	34	37	43	3.7	22.3	72.5	5.9	1.0	3.8	1.0
92RENIN	6.5	39	31	41	22	26	36	3.7	22.3	72.5	6.6	1.0	1.5	1.0

Table 4. Analysis of variance for grain yield, reduction of kernel number (RKN), and reduction of thousand kernel weight (RTKW). Genotypes and environments are considered as fixed effects.

Source of variation		Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Grain yield						
Genotype (G)		3	40.96	13.65	73.6	*
Environment (E)		19	162.75	8.56	46.2	*
	Year (Y)	1	23.91	23.91	128.9	*
	Location (L)	4	51.88	12.97	69.9	*
	Y × L	4	33.19	8.30	44.7	*
	Treatment (Location)	5	43.66	8.73	47.1	*
	Y × T(L)	5	10.09	2.02	10.9	*
Block nested into E		20	5.11	0.26	1.4	
G × E		57	31.95	0.56	3.0	*
	G × Y	3	0.83	0.28	1.5	
	G × L	12	17.83	1.49	8.0	*
	G × Y × L	12	6.68	0.56	3.0	*
	G × T(L)	15	3.65	0.24	1.3	
	G × Y × T(L)	15	2.96	0.20	1.1	
Residual		59	10.94	0.19		
RKN						
Genotype (G)		3	2876.9	959.0	73.3	*
Environment (E)		19	8171.4	430.1	32.9	*
	Year (Y)	1	2423.0	2423.0	185.2	*
	Location (L)	4	3709.0	929.3	70.9	*
	Y × L	4	1193.2	298.3	22.8	*
	Treatment (Location)	5	371.7	74.3	5.7	*
	Y × T(L)	5	474.6	94.9	7.3	*
Block nested into E		20	426.5	21.3	1.6	
G × E		57	3685.4	64.7	4.9	*
	G × Y	3	104.1	34.7	2.7	
	G × L	12	2050.8	170.9	13.1	*
	G × Y × L	12	699.4	58.3	4.5	*
	G × T(L)	15	212.6	14.2	1.1	
	G × Y × T(L)	15	618.5	41.2	3.2	*
Residual		59	772.1	13.1		
RTKW						
Genotype (G)		3	1121.7	373.9	41.7	*
Environment (E)		19	7339.8	386.3	43.1	*
	Year (Y)	1	119.1	119.1	13.3	*
	Location (L)	4	2154.1	538.5	60.1	*
	Y × L	4	1634.2	408.5	45.6	*
	Treatment (Location)	5	2856.8	571.4	63.8	*
	Y × T(L)	5	575.6	115.1	12.9	*
Block nested into E		20	172.7	8.6	1.0	
G × E		57	4523.7	79.4	8.9	*
	G × Y	3	212.1	70.7	7.9	*
	G × L	12	3072.7	256.1	28.6	*
	G × Y × L	12	694.5	57.9	6.5	*
	G × T(L)	15	186.0	12.4	1.4	
	G × Y × T(L)	15	358.5	23.9	2.7	*
Residual		59	528.6	9.0		

* Significant at the 0.05 probability level.

(loading +0.3) increase, GY (loading ~−0.35), RK, SOIrkn, and WDK (loading ~−0.50) decrease. RKm and ARMrkn have low correlation to this component. The component is most heavily weighted by PMK, BK, TALrkn, and WDK. Consistent with the correlations (data not shown), TALrkn is correlated to PMK/BK while the RKN of the other genotypes do not show relationship between these variates.

The plot of individuals on this component orders 91DIJ at the negative end of the component but closely associated with all others except 92REN; 92REN (all treatments) are at the positive end of the component and are noticeably distant from the rest of the individuals on this component. Again, location-year individuals regardless of treatment are relatively closely associated on this component. The component suggests that 92REN is differentiated from the other location-year because of PMK/BK. This is strongly supported by data shown in Table 3.

The second component could be thought of as a climatic axis which arranges environments from humid ones (all treatments of 92REN) with high pressure of powdery mildew and high level of nitrogen to dry ones (all others) with high radiation and water deficits. The site of Rennes is usually known for its humid climate and high pressure of diseases. These results show that to be the case in 1992. Compared with the others, Talent had a particular behavior since it was the most powdery

Table 5. Correlations between grain yield (GY), reduction of kernel number (RKN) and reduction of thousand kernel weight (RTKW). Estimations from 80 genotype × environment combinations.

	GY	RKN
RKN	−0.63*	
RTKW	−0.71*	0.00

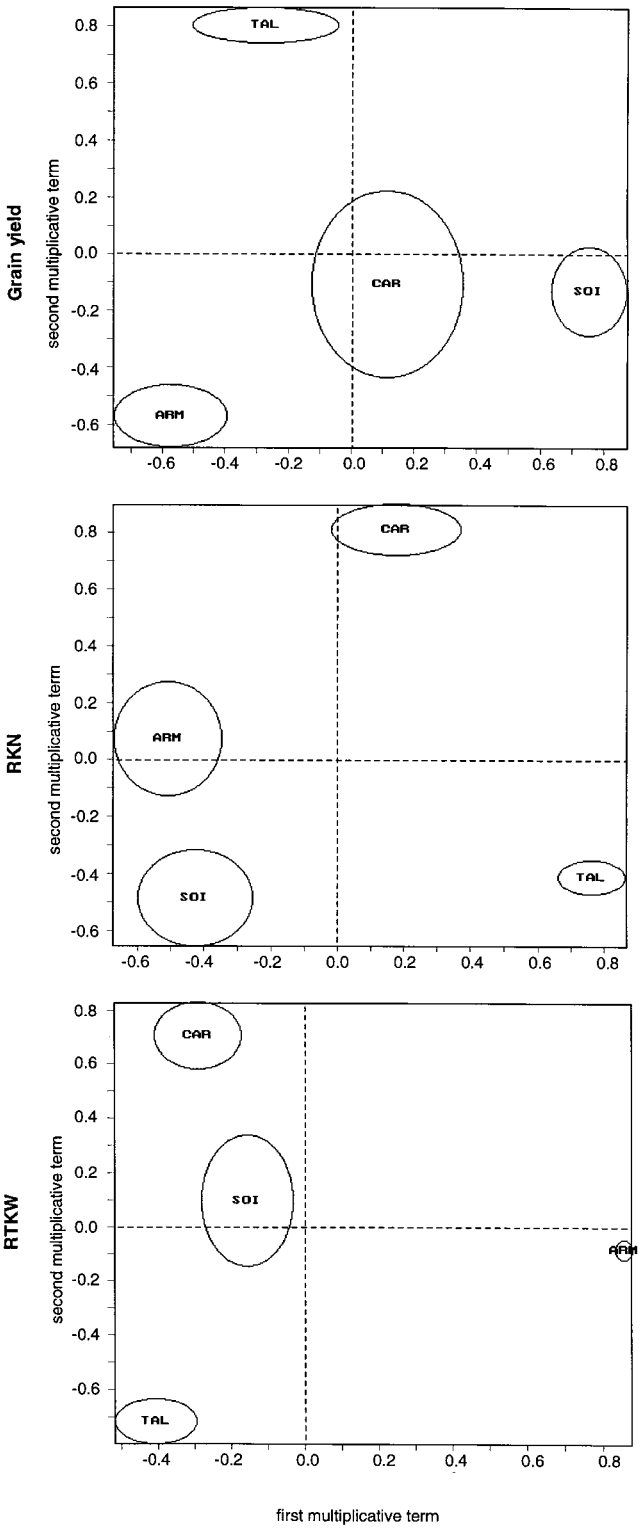

Fig. 3. Multiplicative scores γ_{g1} and γ_{g2} (biadditive model with two terms) for grain yield, reduction of kernel number (RKN), and reduction of thousand kernel weight (RTKW) of the probe genotypes. Indication of the variability of the estimates is given by the ellipses at the 0.05 probability level. TAL = Talent, SOI = Soissons, CAR = Camp-Rémy, and ARM = Arminda.

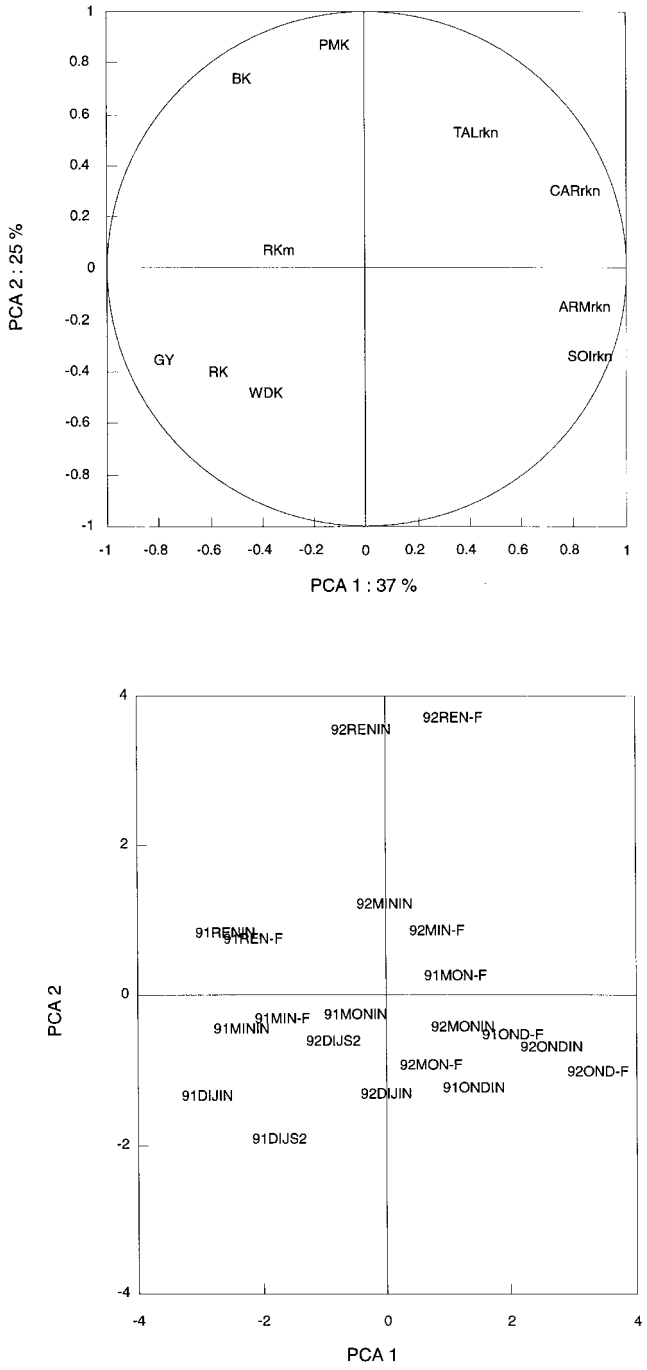

Fig. 4. Principal Component Analysis (PCA) plot of variates related to the grain number formation. PCA loadings for first and second components (top plot). GY = inactive variate (i.e., not used for the determination of the principal components). PCA component scores for year-location-treatment individuals (bottom plot). PCA were performed on correlation matrix.

mildew diseased genotype at 92REN in both treatments (data not shown).

Principal Component Analysis was performed on correlation matrix of variates related to the grain-filling period also (Fig. 5). The first component accounts for 35% of the variance in the correlation matrix. On the plot of variates (top plot), reductions of thousand kernel weight of all genotypes (ARMrtkw, TALrtkw, SOIrtkw,

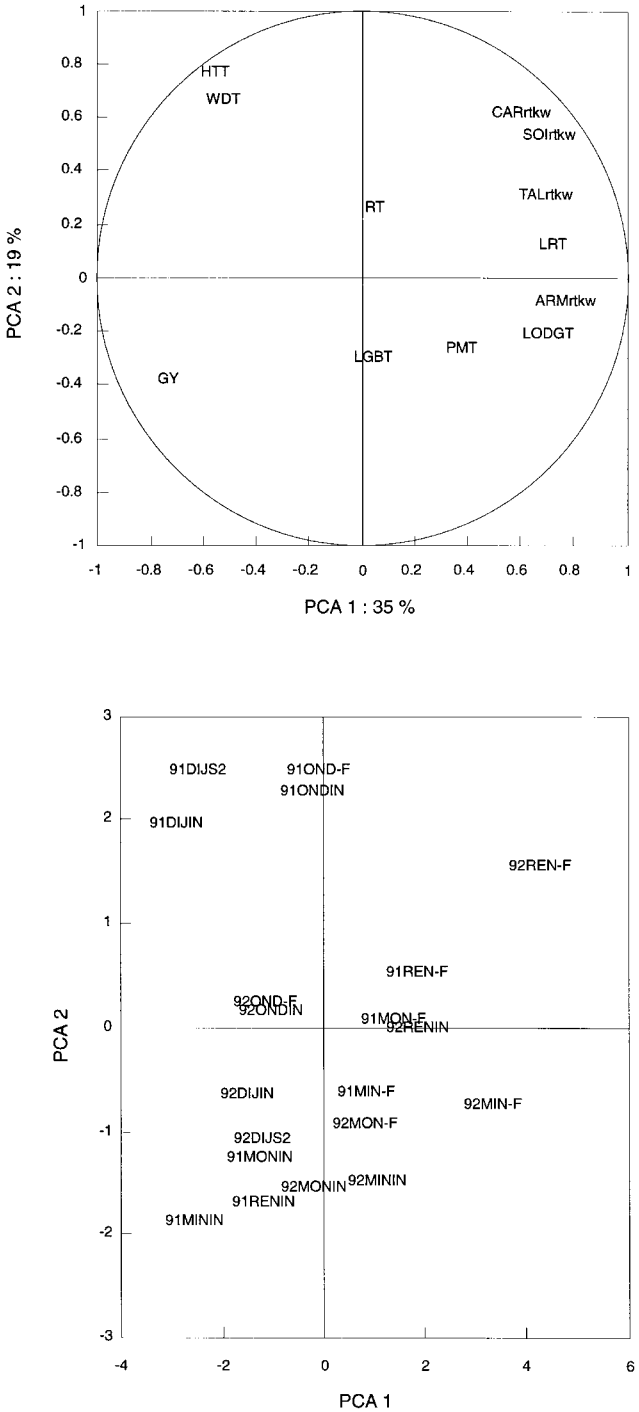

Fig. 5. Principal Component Analysis (PCA) plot of variates associated with the grain-filling period. PCA loadings for first and second components (top plot). GY = inactive variate (i.e., not used for the determination of the principal components). PCA component scores for year-location-treatment individuals (bottom plot). PCA were performed on correlation matrix.

and CARrtkw, loadings ≥+0.55), leaf rust (LRT), lodging (LodgT), and powdery mildew (PMT, loading ~+0.3) increase as water deficits (WDT), high temperature (HTT), and GY decrease. Radiation (RT), and leaf and glume blotch (LGBT) loadings are close to 0 on this component. The plot of individuals on this component (bottom plot) depicts treatments of 91DIJ at the negative end (highest GY, HTT, WDT versus lowest RTKW of all genotypes, LRT, and LodgT) and 92REN−F and 92MIN−F at the positive end (lowest GY, HTT, WDT versus highest RTKW of all genotypes, LRT, LodgT). DIJ and OND individuals, regardless of year and treatment, are closely spaced on this component; other sites show individuals separating on the basis of IN versus −F and year. 92REN and 92MIN shift to the positive side of the component relative to the 91 data; in all cases the REN−F and MIN−F individuals are shifted to the positive end of the component relative to the 91 data; in all cases the REN−F and MIN−F individuals are shifted to the positive end of the component relative to the IN individuals of the same year. The 92MON individuals fall between the 91MON individuals on the component, but in both 91 and 92, the MON−F individuals shift to the positive end of the component relative to the MONIN individuals of the same year (the 92MON exhibiting the least shift).

The second component accounts for 19% of the variation in the correlation matrix; HTT, WDT, CARrtkw, and SOIrtkw (~+0.3 component loadings) increase as PMT, LGBT, and GY (the maximum loading is for GY at ~−0.4) decrease. RT, TALrtkw, LRT, ARMrtkw, and LodgT are weakly related to this component.

Plot of individuals on Component 2 displays 91MININ, 91RENIN, 92MONIN, and 92MININ at the negative end of the component while 91DIJ and 91OND individuals are at the positive end. With the exception of DIJ and OND individuals, this component separates the year and treatment individuals of the other sites in a similar way as the first component. In the case of DIJ and OND, the individuals within a year are not separated by treatment; however, the years for each site are separated on this component. Table 3 indicates that HTT and WDT in 91 were consistently higher than HTT and WDT in 92 at all sites. The table suggests that the within year separation of individuals for MIN, REN, and MON are based on differences of grain yields between IN and −F. In these individuals scores, CARrtkw and SOIrtkw may be playing a part.

These two components could be thought of as a climatic axis which arranges environments from dry and warm ones to humid and cool ones. Humid and cool conditions are associated with diseases and lodging. This is usually met in northern France (Rennes, La Minière, and Mons) and this is supported by the data especially in 1992. It can be noticed also that susceptibility to diseases or to lodging had a greater influence on reduction of thousand kernel weight than did climatic variates. Such a result is new because few attempts were made up to now to compare several yield-limiting factors including disease infections under natural conditions. In such conditions, numerous factors could affect yield and therefore most of them were poorly correlated to grain yield or to reduction of yield components. However, climate can induce indirect effects on other limiting factors such as the level of disease infection. Such interactions between climate and other limiting factors (soil structure, disease damage on plants, and lodging) have been noted by Meynard and David (1992) and Leterme

et al. (1994) in studies of wheat grown in on-farm fields in the western Paris basin. The smaller effect of climatic variates in reducing yield could be due to the fact that only 2 yr were examined and that they were quite similar. Climatic variations were probably not so extreme. That was illustrated by the lack of a cold winter during the study and by the lack of high temperatures during grain filling. In comparison, results reported in the literature were obtained in more extreme conditions. For instance, Stone and Nicolas (1995a, b) studied the effect of short periods of very high temperatures with two varieties differing in heat tolerance. A sudden heat stress from 20 to 40°C enhanced a greater kernel weight reduction (26%) than that resulting from a gradual heat stress of similar thermal time (13%) or equal days treatment (18%). About radiation, Sofield et al. (1977) observed the influence of radiation on growth rate per grain in a two-fold range of natural irradiance. On the other hand, the greater effect of diseases, where no fungicides were used, resulted in a greater reduction in thousand kernel weight which was more severe (24.1% on average) than in the reduction of kernel number (8.0%). These results were partly in agreement with those of Chevalier-Gérard et al. (1994) who found an average yield loss of 26.4% on plots without fungicides and showed that stripe rust, septorias, and powdery mildew were predominant in northern France during 1978 to 1991. In our case, with the exception of stripe rust, disease pressures were similar.

In spite of the small effect of climate, the locations were all different and provided complementary information. Rennes, Dijon, and Ondes were well identified while La Minière and Mons showed similarity.

CONCLUSIONS

One important result is given by the analysis of the yield-component reductions from critical values observed on the four probe genotypes. Critical values for kernel number and thousand kernel weight were first determined with a great accuracy as they constituted basic data for the whole analysis. Our results show that environments can be characterized during the formation of yield, before and after flowering, with the reductions and with indicators of yield-limiting factors.

Nevertheless, our results depended on how climatic indices were defined. For each climatic variate, numerous estimations could be made. At first, we determined several estimates for each one, most of them being closely related to each other (data not shown). For characterizing water deficits, Muchow et al. (1996) compared three indices, a simple index based on rainfall and evapotranspiration, a soil water deficit index, and a relative transpiration index, at two locations in the Australian subtropics for 96 to 101 yr and found differences in grouping of environments. A soil water deficit index based on a soil water balance and a relative transpiration index were better than a simple index. In our study, the criterion was similar to the first of three indices defined by Muchow et al. (1996). Moreover, characterization of the radiation in our study could suffer from inaccuracy because only a fraction of intercepted radiation is absorbed by the crop because part of radiation is lost by reflected and transmitted radiation. However, all genotypes were submitted to the same biases of estimates.

No simulation was used in our study, but instead all analyses were based on experimental data. Improvement could be obtained with simulation by more rapidly providing critical values of components. For instance, Gosse et al. (1986) proposed a model to estimate the potential productivity of a crop from solar radiation intercepted. Similar models may be useful for further investigation of this study. Since experimental data were available, we preferred to analyze them because accuracy could be lost by simulations. When accurate models are available, simulation and experimental approaches to analyze genotype × environment interaction can be compared. In rice (*Oryza sativa* L.), Henderson et al. (1996) used models to simulate water balance, crop growth, and yield and interpreted discrepancies between experimental and simulated data in their study as sources of genetic variation other than phenology. One other further application of this study is to integrate such a characterization of the environments in the analysis of genotype × environment interaction. Such an approach was applied to winter wheat trials to understand genotype × environment interaction and succeeded in providing agronomic explanation with the use of probe genotypes (Brancourt-Hulmel, 1999). This could be extended to newly created genotypes. As emphasized by Bidinger et al. (1996), progress in understanding the environmental control of crop growth and in modeling both environment and crop growth offers real opportunities for a better analysis of crop adaptation.

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REFERENCES

Bidinger, F.R., G.L. Hammer, and R.C. Muchow. 1996. The physiological basis of genotype by environment interaction in crop adaptation. p. 329–347. *In* M. Cooper and G.L. Hammer (ed.) Plant adaptation and crop improvement. CAB International, Wallingford, UK.

Brancourt-Hulmel, M. 1999. Crop diagnosis and probe genotypes for interpreting genotype*environment interaction in winter wheat trials. Theor. Appl. Genet. (in press).

Chevalier-Gérard, C., J.B. Denis, and J.M. Meynard. 1994. Perte de rendement due aux maladies cryptogamiques sur blé tendre d'hiver. Construction et validation d'un modèle de l'effet du système de culture. Agronomie 14:305–318.

Cooper, M., and P.N. Fox. 1996. Environmental characterization based on probe and reference genotypes. p. 529–547. *In* M. Cooper and G.L. Hammer (ed.) Plant Adaptation and crop improvement. CAB International, Wallingford, UK.

Debaeke, P., J. Puech, and M.L. Casals. 1996. Elaboration du rende-

ment du blé d'hiver en conditions de déficit hydrique. I. Etude en lysimètres. Agronomie 16:3–23.
Decoux, G., and J.B. Denis. 1991. INTERA. Logiciels pour l'interprétation statistique de l'interaction entre deux facteurs. Laboratoire de biométrie, INRA, Versailles, France.
Demotes-Mainard, S., G. Doussinault, J.M. Meynard, and Ph. Gate. 1996. Is it possible to diagnose at harvest a problem of pollen sterility in wheat? European J. Agron. 5:169–180.
Desclaux, D. 1996. De l'intérêt de génotypes révélateurs de facteurs limitants dans l'analyse des interactions génotype*milieu chez le soja (*Glycine max.* L. Merill). Thèse de doctorat. Institut national polytechnique de Toulouse, Toulouse, France.
Doré, T., M. Sebillotte, and J.M. Meynard. 1997. A diagnostic method for assessing regional variations in crop yields. Agric. Syst. 54:169–188.
Gate, P. 1995. Ecophysiologie du blé; de la plane à la culture. Lavoisier, Paris.
Gauch, H.G. 1992. Statistical analysis of regional yield trials: AMMI analysis of factorial designs. Elsevier, Amsterdam.
GEVES (Groupe d'Etudes et de contrôle des Variétés et des Semences). 1992. Bulletin des variétés. Céréales à paille. Deuxième partie. Blé, Seigle, Triticale. GEVES, Guyancourt, France.
Gosse, G., C. Varlet-Granchet, R. Bonhomme, M. Chartier, J.M. Allirand, and G. Lemaire. 1986. Production maximale de matière sèche et rayonnement solaire intercepté par un couvert végétal. Agronomie 6:47–56.
Henderson, S.A., S. Fukai, B. Jongdee, and M. Cooper. 1996. Comparing simulation and experimental approaches to analysing genotype by environment interactions for yield in rainfed lowland rice. p. 443–463. *In* M. Cooper and G.L. Hammer (ed.) Plant adaptation and crop improvement. CAB International, Wallingford, UK.
Hunt, L.A., G. van der Poorten, and S. Pararajasingham. 1991. Postanthesis temperature effects on duration and rate of grain filling in some winter and spring wheats. Can. J. Plant Sci. 71:609–617.
Kobata, T., J.A. Palta, and N.C. Turner. 1992. Rate of development of postanthesis water deficits and grain filling of spring wheat. Crop Sci. 32:1238–1242.
Lecomte, C. 1994. Diagnostic agronomique sur les essais inter-stations du groupe céréales. Compte-rendu de la réunion aceintifique du groupe céréales de l'INRA. INRA, Station de Génétique et d'Amélioration des Plantes, Dijon, France.
Leterme, P., H. Manichon, and J. Roger-Estrade. 1994. Analyse intégrée des rendements du blé tendre et de leurs causes de variation dans un réseau de parcelles d'agriculteurs du Thymerais. Agronomie 14:341–361.
Mandel, J. 1971. A new analysis of variance model for non-additive data. Technometrics 13:1–18.
McIntosh, R.A. 1998. Breeding wheat for resistance to biotic stresses. Euphytica 100:19–34.
Meynard, J.M. 1987. L'analyse de l'élaboration du rendement sur les essais de fertilisation azotée. Perspectives Agricoles 115:80.
Meynard, J.M., J. Boiffin, J. Caneill, and M. Sebillotte. 1981. Elaboration du rendement et fertilisation azotée du blé d'hiver en Champagne Crayeuse. II. Type de réponse à la fumure azotée et application de la méthode du bilan prévisionnel. Agronomie 1:795–806.
Meynard, J.M., and G. David. 1992. Diagnostic sur l'élaboration du rendement des cultures. Cahiers Agricultures 1:9–19.
Muchow, R.C., M. Cooper, and G.L. Hammer. 1996. Characterizing environmental challenges using models. p. 349–364. *In* M. Cooper and G.L. Hammer (ed.) Plant adaptation and crop improvement. CAB International, Wallingford, UK.
Oury, F.X., P. Brabant, P. Pluchard, P. Bérard, and M. Rousset. 1990. Etude multilocale de blés hybrides: Niveaux d'hétérosis et élaboration du rendement. Agronomie 10:735–748.
Oury, F.X., P. Brabant, P. Pluchard, P. Bérard, and M. Rousset. 1993. Une étude sur la supériorité des blés hybrides au niveau des capacités de remplissage du grain: résultats d'une expérimentation multilocale. Agronomie 13:381–393.
Robert, N. 1996. Stability of baking quality in bread wheat using several statistical parameters. Theor. Appl. Genet. 93:172–178.
SAS Institute Inc., 1989. SAS/STAT user's guide, Version 6 Cary, NC.
Sebillotte, M. 1980. An analysis of yield elaboration in wheat. p. 25–32. *In* Wheat technical monograph. CIBA-GEIGY, Basel.
Singh, S.D. 1981. Moisture-sensitive growth stages of dwarf wheat and optimal sequencing of evapotranspiration deficits. Agron. J. 73:387–391.
Sofield, I., L.T. Evans, M.G. Cook, and I.F. Wardlaw. 1977. Factors influencing the rate and duration of grain filling in wheat. Aust. J. Plant Physiol. 4:785–797.
Stone, P.J., and M.E. Nicolas. 1995a. Comparison of sudden heat stress with gradual exposure to high temperature during grain filling in two wheat varieties differing in heat tolerance. I. Grain growth. Aust. J. Plant Physiol. 22:935–944.
Stone, P.J., and M.E. Nicolas. 1995b. Effect of timing of heat stress during grain filling on two wheat varieties differing in heat tolerance. I. Grain growth. Aust. J. Plant Physiol. 22:927–934.
Trottet, M. 1997. Etude du progrès génétique et de la rusticité des variétés de blé tendre et recherche de variabilité pour ce caractère permettant d'orienter la création variétale dans le cadre d'une agriculture faibles intrants. p. 64–68. Compte-rendu de la réunion scientifique du groupe céréales de l'INRA. INRA, Unité de Génétique et d'Amélioration des Plantes, Mons, France.
von Wricke, G. 1962. Über eine Methode zur Erfassung der ökologischen Streubreite in Feldversuchen. Z Planzenzücht 47:92–96.
Webb, A. 1972. Use of the boundary line in the analysis of biological data. J. Hort. Sci. 47:309–319.
Wiegang, C.L., and J.A. Cuellar. 1981. Duration of grain filling and kernel weight of wheat as affected by temperature. Crop Sci. 95–101.