Towards a global characterization of winter wheat cultivars behavior in response to stressful environments during grain-filling

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Highlights:

- A multi way characterization of cultivar response to foliar diseases is proposed
- No trade-off between tolerance and productivity or disease susceptibility was observed
- Alternative characterization by remote sensing rather than sampling is considered

Summary
Starting from grain yield, quality and resistance against multiple diseases, the characterization of the cultivar's behavior increased in recent decades. Needs in quantitative assessments of a larger range of criteria has greatly evolved towards yield stability in a large range of fluctuating environments. Using a large dataset crossing cultivars and environments, we thus explored the relationships between yield and Healthy Area Duration (HAD), as affected by genotype, environment and septoria caused by *Zygmoseptoria tritici*. A set of indexes was then proposed to properly profile cultivar's behavior. A curvilinear relationship relating HAD to potential yield was first parameterized. It allows quantifying HAD efficiency. Susceptibility (HAD loss) was differentiated from total tolerance (the ratio between yield loss and HAD loss). Finally the specific tolerance, i.e. not due to HAD level, was quantified. Correlations between indexes pointed out that no trade-off was shown between total tolerance and actual or potential yield as well as disease susceptibility. These correlations partially depended on the nitrogen status of crops, underlining other *G×E* interactions indexes may trap. Finally, as HAD efficiency appeared more highly linked to actual yield than potential yield we proposed an alternative set on indexes based on Healthy Area Absorption (HAA) that accounted for meteorological variability. Interestingly, these last indexes were insensitive to nitrogen nutrition as well as to cultivar susceptibility to *Z. tritici*. The developed indexes allowed profiling the cultivars' behavior under a common range of environments. HAA-based indexes open the way to a useful global characterization of cultivars by breeders. Moreover, HAA can be assessed using high-throughput phenotyping tools. A thorough evaluation of this last point needs to be done.

Key words:
Resistance, tolerance, escape, ecological strategies, indexes, traits

1. Introduction

Identifying cultivars that best match production objectives of different users is a key point of seed sector. Because each cultivar expresses its potential in a restricted range of favorable environments (Meynard and Jeuffroy, 2006), farmers choose cultivars adapted to their location. Therefore, characterization of cultivars' behavior has greatly evolved in recent decades, involving a larger range of criteria, moving from grain yield to quality, resistance against multiple diseases, and yield stability in a large range of environments (Reynolds *et al.*, 2012). Registration and evaluation of new cultivars mobilize large geographical networks of experimental trials to better characterize genotype x environment (*G×E*) interactions. However, for economic reasons, multi environment, multi genotype trials hardly allow a fine description of traits of interest (Lecomte *et al.*, 2010; Sadras and Slafer, 2012). As environmental situations were shown to represent up to 75% of *G×E* yield variations (Lecomte et al. 2010; Casadebaig *et al.,* 2016), research and development has focused rather on optimizing geographical networks than on diversifying G criteria (traits) to better characterize the cultivars (Chenu et al., 2011; 2017). However, optimizing such networks of trials is impaired as climate change reconfigures the distribution of the environments and thus imposes a continuous adaptation of networks in target populations of environments (Chenu *et al.,* 2017). In a stable environment, the attainable yield is the simplest way to compare cultivars; therefore, yield remains the main criterion to succeed the registration of new wheat cultivars. However, climate change also induces a fluctuating context that enlarges uncertainties in attainable yields because crops experience an increased number of multi stress episodes (Brisson *et al.*, 2010), compounded by reduction of agronomic inputs linked to environmental concerns. In highly unpredictable stressful environments, the need to conceive easy-to-use designed tools to compare cultivars in fluctuating contexts thus emerged. Breeders also may have to propose yield insurance rather than yield potential, highlighting the need to combine different crop

strategies that may attenuate the effect of stress episodes.

Ney *et al.* (2013) listed such strategies that either, shift critical development stages to unstressed environments (escape strategy), decrease symptoms expression while exposed to a same stress (resistance strategy) or allow symptoms' development but limit their impact on yield or quality (tolerance strategy). Both escape and resistance can be addressed by modifying a few genes and have therefore received large attention. These strategies involving traits governed by qualitative resistance genes result in a rapid and efficient breeding. Yet climate change challenges escape strategies while resistances may be circumvented if a low number of resistances or cultivars are widespread in the landscape (Goyeau and Lannou, 2011; Papaïx *et al.*, 2018). The complementary use of indirect quantitative traits, often a mixture of quantitative resistance and tolerance traits (Restif and Koella, 2004; Nunez-Farfan *et al*., 2007) could help delaying the circumvention of resistances while buffering yield losses.

Although Parker et al. (2004) have suggested that tolerant traits are heritable and complementary to resistance traits, two potential drawbacks have currently limited the identification and use of tolerant cultivars by breeders. First, as tolerance allows epidemics to develop the resulting increase in inoculum pressure was perceived as a threat that higher risks of crop losses may occur. However, Espinosa and Fornoni (2006) have shown that tolerance has no selective effect on pathogen fitness. Espinosa and Fornoni (2006) also pointed out the expression of tolerance depends on both inoculum load and *G×E* context. Therefore, tolerance would benefit to be associated to other strategies to attain sufficient efficacy. Secondly, tolerance has been suspected of being limited to cultivars with low potential yields. Such low yielding cultivars rather exhibited a low responsiveness to high yielding conditions than a protection against stressful environments (Ferrante et al., 2017). Though frequently examined, no trade-off of tolerance to yield has been demonstrated so far (Foulkes et al., 2006; Bancal et al. 2015; Collin et al., 2018), but the compromise between productivity and tolerance have to be ascertained thoroughly so that tolerance be an adoptable trait by breeders. A sufficient range of *G×E* combinations is therefore needed to address the question of using tolerance traits to face the increased climate variability without disadvantaging productivity.

The quantification of tolerance must also be improved. According to Ney *et al.* (2013), tolerance is defined from the relationship between symptoms (i.e. loss of green area) and yield. Johnson (1992) followed by Paveley *et al.* (2001), Parker *et al.* (2004) and Foulkes *et al.* (2006) related the loss in healthy area duration (HAD) to that of yield. However, Gate *et al*. (2006) observed that yield is not proportional to HAD; instead yield asymptotically reaches a maximum level at higher HAD. They therefore suggested that crops with high HAD, thus with high yield potential, could be more tolerant to stress, as a HAD loss does not imply a yield loss. HAD could be increased either through delayed senescence (assessed by senescence time, as defined below) or through leaf area (assessed by maximal leaf area index). Bancal *et al.* (2015) verified that senescence time is a suitable candidate for tolerance trait. Conversely, if HAD increases with higher leaf area indexes, the crops are also more susceptible (less resistant or escaping) to diseases. Hence, susceptibility and tolerance should not be regarded separately. This points out that cultivars should not be characterized by traits only linked to a single strategy of response to stresses, but rather by a cultivar behavior, i.e. a set of traits that somehow accounts for the relationships between yield, susceptibility and tolerance according to environment (Gouache *et al.*, 2014).

Based on this rapid literature review, the need to better characterize behavior of cultivars in varying environment emerged. Tolerance had been largely dismissed and consequently not directly selected by wheat breeders, thus probably limiting the yield insurance (and stability) in fluctuating environments. For instance, breeding has progressively increased the grain number per square meter in UK cultivars (Shearman, 2015). The resulting reduction in the degree of grain-source saturation (a tolerance trait; Collin *et al.*, 2018) would explain tolerance decline with release year (Foulkes *et al.*, 2006). To better address the question of trade-off among characteristics of cultivar behavior, we thus focused on disease tolerance and explored its relationships to yield and resistance. Using an unbalanced database originally built to study tolerance of wheat cultivars to Septoria leaf blotch (*Zymoseptoria tritici*), the aim of the present study was to propose a set of indexes to characterize cultivars' behavior in varying environment: potential yield, HAD efficiency, susceptibility, total and specific tolerance to stresses. The trade-offs between these indexes were then analyzed as well as the interest in breeding for tolerance. We finally proposed a simplified assessment of cultivar behavior in a perspective of high throughput phenotyping by breeders.

2. Materials and methods

2.1 Dataset

Observations came from a complex dataset fully described elsewhere (Bancal *et al.*, 2015) that pooled three experiments carried out in France to analyze damage impacts of different septoria epidemics on wheat yield in France. The main pest affecting crops was always identified as Zymoseptoria (previously Septoria) tritici: other diseases may also have

occurred, but their severity remained low compared to septoria epidemics.

The structure of data is complex, as commonly observed in meta-analysis; further in paper, each combination of one year, one location, one fertilizer management and one cultivar was referred to as a trial. Briefly, expt A yielded 65 trials without overall design over a single location, seven years, nine cultivars and three fertilization levels. Expt B yielded 36 trials on a single location (seven cultivars, three years and two fertilisation levels). Expt C yielded 60 trials over five locations (9 cultivars, two years and one fertilisation level). Both expt B and expt C included a subpart balanced in terms of year, location, cultivar and fertilisation.

A total amount of 101 trials received a standard fertilization with high nitrogen inputs calculated using the balance sheet method (Makowski *et al.*, 1999). Additionally 43 trials experienced light nitrogen shortage (up to 6 $g \cdot m^{-2}$ below the standard nitrogen fertilization, or suboptimal date of fertilizer application). Lastly, 17 trials experienced a severe nitrogen deprivation (14 $g \cdot m^{-2}$ below the standard nitrogen fertilization).

The aim of this article was not to classify cultivars, but rather to provide a set of indexes characterizing their response to the biotic environment. Thus, the dataset was used as a whole to benefit from the wide *G×E* range when otherwise it would have been subdivided into balanced items. Note that natural epidemics cannot be reproduced in the field either. As a result, field-scale epidemics rarely match the requirements for normality, a difficulty for an unbiased, overall comparison. This is why this article aims at defining tools based on paired sub-trials for such a characterization. Under this purpose, the main need was to increase the dataset. Therefore, despite its complex structure with treatments that could lead to bias between experiments, the dataset was analyzed as if it were random by working approximation.

Despite they result from independent experiments, all data shared a common point. Each trial was repeated in two paired sub-trials, themselves averaging two or three plot repetitions. The first sub-trial was grown with full fungicide protection according to local practice, whereas the second sub-trial was unprotected against leaf pathogens, thus permitting the development of disease according to natural epidemics. The systematic presence of paired sub-trials in trials was a powerful statistic tool, as the complex structure of data did not permit an overall study of the effect of genotypes and *G×E* interaction.

2.2 Green Area Measurements

As often in meta-analyzes, measurement methods varied between experiments. LAI (total area of leaf blades per soil m^2) was always measured on a sample of at least one third of square meter, using scanner or planimeter. The leaf layers (i.e. the top leaf, the 2nd leaf and so on) were separated in each experiment. Thus green area fraction (gf), i.e. green to total area of leaf blade was measured in each leaf layer. Depending of experiments, gf was either visually assessed using a reference picture-scale, or measured by image analysis of scanned blades. The evolution of gf was recorded by repeated assessments during grain filling (four to seven, depending of experiment). To account for temperature changes according to trials, gf was plotted against degree-days after heading ($°Cd_H$). Because the sampling schedule was not the same depending of experiment, integration by triangulation could bias comparisons. Instead, as gf followed a sigmoid shape over time, its evolution per treatment was then fitted to Gompertz equations from heading date until harvest (Bancal et al., 2015); the integral of which was multiplied by LAI in each leaf layer to calculate HAD (in degree-days after heading by m^2 of leaf area per m^2 of soil; $°Cd_H \cdot m^2 \cdot m^{-2}$). The procedure was detailed in supplemental data 1.

2.3 Boundary line of yield to HAD relationship

The entire dataset was used to establish an upper boundary line of yield to HAD relationship. Regardless of fungicide protection or nitrogen fertilization, the maximum yield reached for each HAD followed a saturating shape that was fitted by quantile regression to obtain an equation of the boundary line (Makowski *et al.,* 2007). Fitting was obtained by non-linear algorithms, using R version 3.5.1 (R Core Team, 2018), with quantreg package version 5.36 (Koenker, 2018). Beforehand the best centile value was determined among 80th to 99th ones, as the method was found very sensitive to a slight overestimation. The 87th centile gave the best compromise between a high quantile value and a sufficient precision of parameter estimation for the following equation (1):

$$P = 1091 \cdot [1 - \exp(-1.22 \cdot 10^{-3} \cdot HAD)] \quad (1)$$

where P ($g \cdot m^{-2}$) is the potential yield that can be reached at any HAD.

The observations were not independently distributed but structured by genotype, location and year. It gives rise to random effects (main effects and interactions) that would need to be taken into account. Genetic effects and *G×E* interactions could be taken into account by two ways: (1) by estimating their distance to a common trend, or (2) by establishing a panel of specific trends per genotype and/or environment. This second way needs a very large number of data for each genotype or *G×E*, which was out of reach with sampling methods. The first way was thus followed, considering that the very definition of an upper boundary line does not exclude it could be universal, thus independent of genetic and *G×E* effects. The distance of actual yield to boundary line at a given HAD represented the conversion efficiency of HAD into yield (HADE), which was calculated as the ratio of actual yield (Y) to potential yield (P):

$$HADE = Y/P \quad (2)$$

2.4 Intolerance calculations

In this paper, we focused on post heading stresses inducing a loss in green area due to septoria epidemics. When crops were exposed to such stress, their canopy was reduced. Then a third index assessed the apparent sensitivity to stress given by the HAD loss (ΔHAD; in °Cd·m^2·m^{-2}) linked to stress exposure:

$$\Delta HAD = HAD_{unprotected} - HAD_{protected} \quad (3)$$

The loss of HAD between protected and unprotected sub-trials generally led to a loss of yield (ΔY; in g·m^{-2}), after modulation by crop tolerance. In literature, intolerance, rather than tolerance, is calculated: in other words, the lower the value the higher the tolerance. Total intolerance (g·°Cd^{-1}·m^{-2}) was estimated for each paired trial by the following ratio:

$$Int_T = \Delta Y / \Delta HAD \quad (4)$$

Eleven paired trials showing negligible HAD losses (below 5% of protected HAD) were thus discarded from intolerance calculation to avoid mathematical indeterminacy.

The derivative of equation (1), dP/dHAD, gives the part of intolerance directly linked to crop HAD, regardless of genotype, environment or crop management. Conversely, a specific intolerance Int_S, was also calculated as the intolerance left once HAD impact on Int_T was taken into account:

$$Int_S = (\Delta Y - \Delta P) / \Delta HAD \quad (5)$$

Thus, specific intolerance contributes to a variable extent to total intolerance that was examined further.

2.5 HAA simulation

Methods based on either imagery or hyperspectral radiometry are currently developed to assess the light absorption by the canopy and could become useful since intercepted radiation is linearly related to yield (Monteith and Moss, 1977). Remote sensing methods are not presented here, as remote sensing data were neither available in A, B or C expts. Instead, intercepted radiation was simulated, using the model describing the daily interception of incoming PAR proposed by Jones (2014).

$$\text{Daily Interception} = 1 - \exp(-0.68 \cdot LAI) \quad (6)$$

The top leaves, which received most radiation, usually senesced latter that the bottom leaves. Therefore, the reliability of interception by green tissues was increased when accounting for this stratification. The procedure is detailed in supplemental data 2; it used the Gompertz fit of the green fraction in each leaf layer, as described before. Self-shading of lower leaves by top leaves was taken into account according to Bancal et al. (2007).

After that, Healthy Area Absorption (HAA) was obtained by integration of the radiation intercepted by green tissues from heading until harvest.

Two additional indexes based on HAA-Yield relationship were then defined to foreshadow what could be done in the future when comparing genotypes with remote sensing data. First, HAA-intolerance (Int_A; in g·MJ^{-1}) was analogous to HAD-intolerances previously defined:

$$Int_A = \Delta Y / \Delta HAA \quad (7)$$

The second index was based on the observed linear relationship between HAA and Yield, regardless of fungicide protection or nitrogen fertilization. Using Reduced Major Axis regression (Smith, 2009), the whole dataset was fitted to the following equation:

$$Y = 2.08 \cdot HAA + 83.0 \quad (8)$$

For any trial, a Yield-Radiation Deviation (YRD) was then defined as the difference between observed yield and predicted yield derived from the previous equation:

$$YRD = Y - 2.08 \cdot HAA - 83.0 \quad (9)$$

Then YRD represents the deviation from HAA driven yield variation.

2.6 Statistical analysis

All statistical procedures were carried out using the Statgraphics Plus program (Manugistics, Inc., Maryland, USA) with an overall error rate of $\alpha = 0.05$. The normality of each index was assessed on the whole dataset, using skewness and Kurtosis tests. Discarding the 17 trials grown under severe nitrogen deprivement, yields, HAD and HAA were normally distributed regarding the remaining 144 trials. Intolerance calculation had also required discarding some trials (see section 2.4), and for these indexes the statistics applied to the remaining 136 trials. Thereafter, as data is structured by genotype, location and year, the independence assumption was not strictly met in this complex dataset (Piepho, 2018). However, as the results mainly focus on the building of indices, the significance of the correlations between indexes was nevertheless mentioned. Conversely, as natural epidemics do not follow a normal distribution, because of too few trials per genotype, normality was violated within most of genotypes. Therefore, any overall study of G or E effect was precluded. However, it does not exclude pairwise comparisons, which was then used to compare the indexes of two cultivars in a range of environments. In most cases, differences between cultivars fulfilled the requirements of normality, and t-test was used; alternatively, rank and sign tests were used.

Most of the reported correlations were obtained using the usual method of ordinary least squares (OLS), the significance of which could be tested from their correlation coefficient, considering as underlined previously, that the conditions of independence and randomness of the variables are not strictly fulfilled by the database. In the particular case of the relationship between HAA and yield, we used a reduced major axis regression (RMA) instead of the OLS method (Smith, 2009). This method does not allow the subsequent calculation of correlation

coefficient, but it greatly reduces the bias when both abscissae and ordinates are obtained by measurements. By construction RMA regression line faithfully follows the major axis of the scatter plot, which was necessary to obtain the equation (8).

3. Results

3.1 Raising the difficulties when comparing the behavior of cultivars

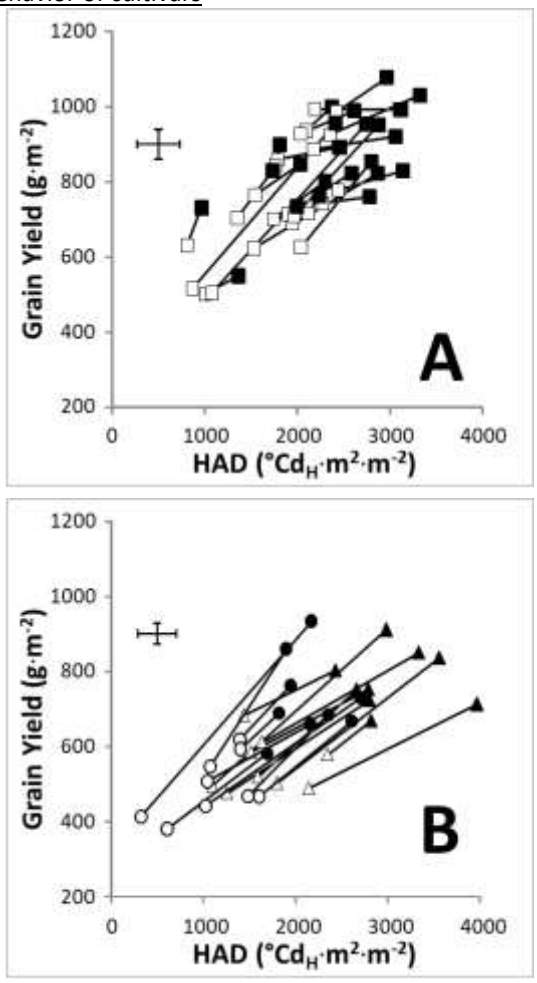

Figure 1: Effect of fungicide protection on HAD and grain yield on wheat cultivars.
In fig. 1A the wheat cultivar Soissons (squares) was grown in 23 trials differing by year, location and fertilization; in fig. 1B the cultivars Apache (triangles) and Charger (circles) were both grown in the same nine environments differing by year or location with optimal fertilization. In each trial, paired sub-trials were obtained with (closed symbols) or without (open symbols) fungicide protection against leaf pathogens. The points corresponding to paired sub-trials in a trial are linked together, and the slope indicates the level of intolerance to the disease. The average standard deviation for HAD and yield between replicates in a sub-trial was reported in the upper left corner.

Figure 1A shows HADs and yields of the cultivar the most represented in the database, Soissons, which was grown in 23 trials differing by year, location and fertilization. In each trial, paired sub-trials were obtained either applying or not fungicide protection against leaf pathogens. Yield in protected sub-trials ranged from 550 to 1076 $g \cdot m^{-2}$, so that some of them can nevertheless be regarded as stressed. Those uncontrolled abiotic stresses (water, irradiation, temperature, nitrogen etc.) cannot be studied per se; they nevertheless generated a welcomed variability. Depending on the trial, HAD losses by disease ranged from 46 to 1669 $°Cd_H \cdot m^2 \cdot m^{-2}$, corresponding to yield losses from 0 to 450 $g \cdot m^{-2}$. Accordingly, the total intolerance calculated by equation (4) ranged from 0.04 to 0.74 $g \cdot °Cd^{-1} \cdot m^{-2}$ with a median at 0.15 $g \cdot °Cd^{-1} \cdot m^{-2}$. However, this variability is far from random, as shown in the figure 1A where total intolerance is illustrated by the slope between paired sub-trials. The higher the HAD of the protected sub-trial, the lower the intolerance to disease. (r= -0.65, data not shown). Consequently, total intolerance cannot be regarded as a genetic constant, it is also affected by the HAD the cultivars build in a given environment.

To account for genotype × environment (*G×E*) effects on tolerance, unprotected sub-trials were compared to protected sub-trials over several years and locations. Figure 1B shows the results of paired sub-trials for Apache and Charger cultivars grown in nine locations × years, under optimal fertilization, using a small balanced sub-database. Cultivars however did differ not only in tolerance, but also in yield in protected sub-trials, and in disease severity (ΔHAD). The question then becomes: how to compare cultivars' tolerance with all components varying at the same time? In addition, these nine environments did not provide a sufficient number of situations to allow random environmental variability to meet the normality assumption, thus limiting statistical comparisons. Consequently, a new conceptual framework was needed to help analyzing the cultivars' behavior under different stressful environmental conditions.

3.2 Curvilinear relationship between HAD and potential yield

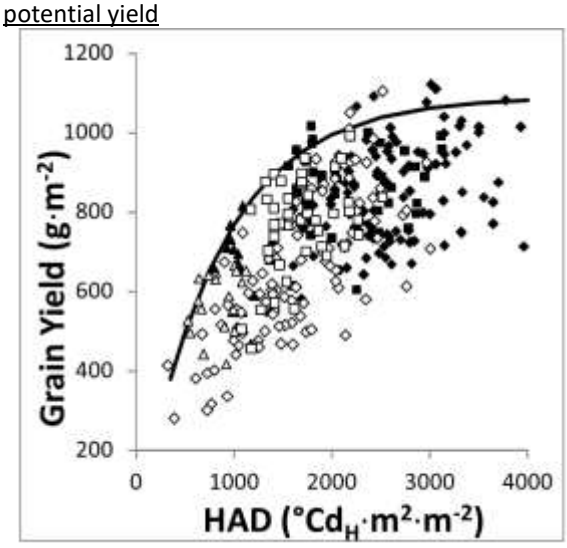

Figure 2: HAD to grain yield relationship in wheat crops
The figure reports the results for the whole data set: 161 trials involving 18 cultivars and three levels of nitrogen deprivation by nitrogen fertilization: optimal (diamonds), moderate (squares)

or severe (triangles). In each trial, paired sub-trials were obtained with (closed symbols) or without (open symbols) protection against leaf pathogens. The curve of potential yield, obtained by nonlinear quantile regression (see equation (1) in text), is reported as plain line.

Figure 2 relates HAD to yield in 161 trials that were carried out using 18 cultivars over many years, locations and fertilizations. Some cultivars were grown in the same environment (e.g. Fig. 1B), others not, which precludes any overall comparison. In protected sub-trials, indicated by closed symbols, cultivars showed differences in their source potential (i.e. achieved HAD), and also in their efficiency in converting HAD to yield (HADE). Both protected HAD and HADE were affected not only by the genotype, but also by the environment (Fig. 1A), leading to a large dispersion of dots drawing protected sub-trials. Finally, yield correlated moderately with HAD (r=0.32). In unprotected sub-trials HAD decreased more or less, and its correlation to yield increased (r=0.66). However, the data ranges of protected or unprotected sub-trials overlapped widely (figure 2), suggesting the relationship of HAD to yield followed a same trend regardless of fungicide protection. The yield increased very rapidly with HAD below about 2000 °$Cd_H \cdot m^2 \cdot m^{-2}$ then showed a clear tendency to saturate at higher HAD. Regardless of trial or fungicide treatment, the maximum yield reached for each HAD followed a saturating shape, which was fitted by non-linear quantile regression to the equation (1). The corresponding curve is reported as 'potential yield' (P) in Fig. 2, an upper limit for grain yield that is assumed as independent of both genetic and *G x E* effects. The ability of any genotype to approach P in a given environment is indicated by HADE, according to equation (2).

When the disease decreased HAD in unprotected sub-trial as compared to protected sub-trial, the curve of potential yields was never crossed. Thus, any trial with a high HAD under full fungicide protection could maintain a high P even without fungicide protection, provided that unprotected HAD remained higher than 2000 °$Cd_H \cdot m^2 \cdot m^{-2}$. Conversely, a trial with a low HAD under fungicide protection could not maintain a high P when disease decreased HAD, regardless of genotype, because P fell sharply when HAD was lower than 2000 °$Cd_H \cdot m^2 \cdot m^{-2}$. Finally, in trials with high HADE, the tolerance was mainly limited by the curve of potential yields. However, HADE of protected trials was often rather low, either due to environment (Fig. 1A) or to genotype, so that a new framework is needed to study tolerance in such cases.

3.3 Defining indexes from HAD to identify profiles of cultivar behavior.

We then proposed the five following indexes to describe the different behaviors of cultivars; figure 3 further shows graphically their significance.

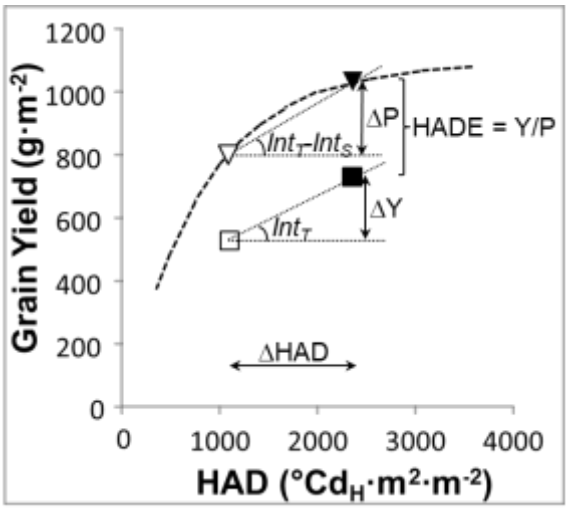

Figure 3: Indexes characterizing cultivar behavior from HAD-Yield relationship.

Paired sub-trials managed with (closed symbols) or without (open symbols) protection against leaf pathogens show the different indexes. HAD is in abscissae, while ordinate reports either actual yields (Y, squares), or potential yields (P, triangles) on the potential curve in dashed line. The ratio of actual yield to potential yield is HADE, while the slope ΔY / ΔHAD is total intolerance (Int_T). Specific intolerance Int_S represents the part of intolerance that remains once HAD impact on Int_T has already been taken into account: $Int_S = (\Delta Y - \Delta P) / \Delta HAD$.

Firstly, the green area was characterized by HAD, and therefore the potential yield (P) was defined as the maximum yield attainable at a given HAD according to equation (1). The second index quantified the efficiency to convert HAD into yield by the ratio of actual yield to potential yield (HADE) according to equation (2). The third index assessed the apparent sensitivity to stress given by the HAD loss linked to stress exposure (ΔHAD) according to equation (3). Finally, two kinds of intolerance could then be defined using or not the potential curve. Total intolerance (Int_T) was calculated from the ratio of yield loss to HAD loss, according to equation (4). Literature commonly characterizes Int_T only; however due to the curvilinear relation between potential yield and HAD, a part of intolerance simply results from actual HAD values, regardless of other *G×E* features. A specific intolerance index (Int_S) has therefore been constructed to be as independent as possible from actual HAD. Thus, Int_S represents the part of intolerance that remains once HAD impact on Int_T was already taken into account: $Int_S = (\Delta Y - \Delta P) / \Delta HAD$, according to equation (5). The results presented below focus on both total and specific intolerances (Int_T and Int_S, respectively), and yield.

3.4 Illustrating tolerances in two contrasted cultivars

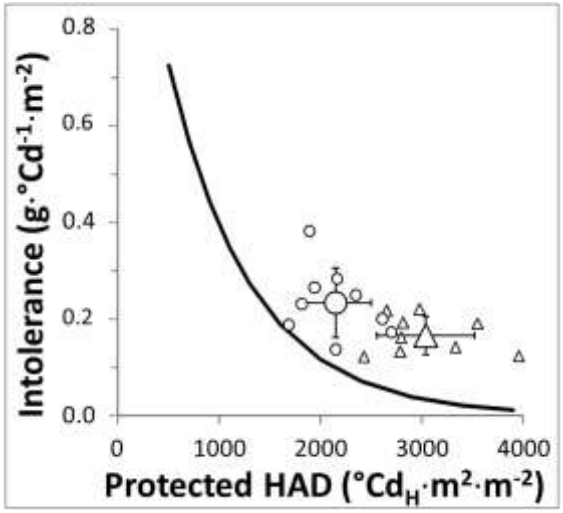

Figure 4: HAD and total intolerance of cultivars shown in figure 1B.
Small symbols (triangles for Apache and circles for Charger) indicate the results for each of the nine environments differing by year or location. Big symbols are the genotype average with bars indicating standard deviation. The line shows the derivative dP/dHAD of equation (1). It indicates the direct effect of HAD on intolerance.

The indexes were first calculated in the case of the two cultivars Charger and Apache previously shown in figure 1B. All indexes met the normality hypotheses and were then compared using paired test that accounted for environment variability. In protected sub-trials, the potential yield reached by Apache (1061 ±15 g·m^{-2}) was significantly higher ($P < 10^{-3}$) than that reached by Charger (1006 ±34 g·m^{-2}), due to the higher HAD in Apache than in Charger ($P < 10^{-3}$). However actual yields were lower than potential yields and hardly different ($P < 0.05$) regarding the cultivars (779 ±77 vs. 730 ±109 g·m^{-2} for Apache and Charger respectively). A lower HAD efficiency could therefore be suspected in Apache, but HADE values were too variable according to environment to be shown significantly different between genotypes (0.73 ±0.09; $P > 0.05$). Susceptibility indicated by HAD losses in unprotected crops was significantly higher in Apache (1392 ±476 vs. 1044 ±471 °Cd·m^2·m^{-2}; $P < 0.05$), but yield losses were not (233 ±111 g·m^{-2}; $P > 0.05$). Total intolerance Int_T was calculated in each year and location, and compared to HAD of the protected crop (Fig. 4). Figure 4 also permitted an assessment of specific intolerance Int_S by the distance to the reported derivative of the yield potential curve. No significant difference in Int_S was shown between the two cultivars (0.05 ±0.08 g·°Cd^{-1}·m^{-2}; $P > 0.05$). Therefore the higher total intolerance Int_T observed for Charger (0.17 ±0.04 vs. 0.23 ±0.07 g·°Cd^{-1}·m^{-2}; $P < 0.05$), was fully accounted for by its lower HAD under fungicide protection.

3.5 Trade-off between yield and tolerance indexes?

Table 1: Correlations to actual and potential yields of indexes characterizing the profile of cultivar behavior

	Correlation to actual yield Y		Correlation to potential yield P	
	All data	N-deprivment retired	All data	N-deprivment retired
Protected HAD	0.45 ND	0.23 *	0.89 ND	0.94 ***
Protected Y	–	–	0.48 ND	0.20
Protected HADE	0.84 ND	0.96 ***	-0.06 ND	-0.10 ns
Protected P	0.48 ND	0.20	–	–
HAD loss	0.15 ND	-0.01 ns	0.51 ND	0.54 ***
Y loss	0.15 ND	0.04 ns	0.26 ND	0.25 *
Total intolerance	-0.04 ND	0.05 ns	-0.48 ND	-0.32 **
Specific intolerance	0.40 ND	0.24 *	0.32 ND	0.17 ns

The significance of correlations obtained within the whole dataset cannot be determined. Discarding 17 trials grown under severe nitrogen deprivement, data was normally distributed in the remaining trials, and the significance of correlations under normality requirements is reported (***: $P < 10^{-4}$; **: $P < 10^{-3}$; *: $P < 0.01$; ns: $P > 0.05$; ND: not determined).

The preceding example showed that the five proposed indexes might help comparing cultivars' behavior while considering environment variability. We thus calculated indexes for the whole dataset, but we have to discard 17 trials severely deprived in nitrogen, to reach the normality requirements helpful in statistical analyses. Actually the discarded trials exhibited very low HAD even in protected sub-trials, and would not be regarded as unstressed control by breeders. A first key point was then to identify if a trade-off did exist or not between tolerance indexes and actual or potential yield. Table 1 thus summarizes the obtained correlation coefficients between the different indexes and either yield or yield potential.
The actual yield hardly correlated to source indexes HAD and P, with correlation coefficients at 0.2 ($P \approx 0.01$). The best predictor for yield in protected sub-trials was not HAD, but its conversion efficiency HADE ($r > 0.8$; $P < 10^{-4}$). No correlation was observed between protected yield and either disease susceptibility (ΔHAD), or yield loss or even total tolerance, Int_T. However specific intolerance Int_S significantly increased with yield ($P < 0.01$). Correlations to potential yield P markedly differed from those to actual yield Y. As P was calculated from HAD according to equation (1) the high correlation coefficient between HAD and P is thus quite trivial. More interesting was the absence of significant correlation of P to HADE, contrasting with the very tight correlation of actual yield to HADE. Lastly high levels of potential (in other words, high HAD values) decreased Int_T, while they had no effect on Int_S. However high levels of P also led to high HAD losses ($r=0.54$; $P < 10^{-4}$), and high yield losses ($r=0.25$; $P < 0.01$) in unprotected sub-trials.

3.6 Towards HAA-based indexes

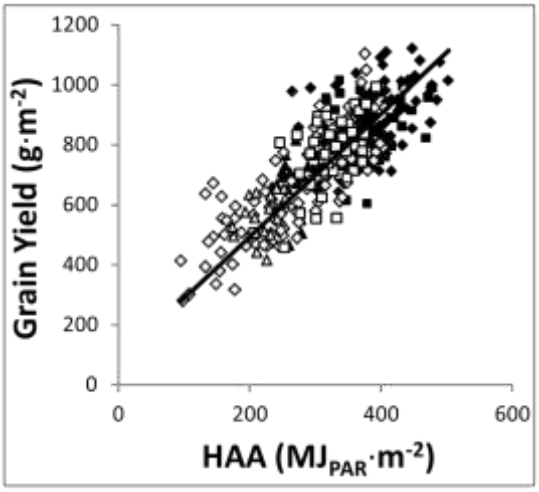

Figure 5: Cumulative intercepted radiation by green leaf area after heading (HAA) and grain yield in wheat crops.
Symbols are as in figure 2. The linear RMA correlation is reported

Figures 1 and 2 showed that HADE markedly changed according to year and location, which is partly due to the local variability of incoming radiation. This variability was not taken into account when characterizing the crop source by HAD, whereas it can be achieved by using the sum of radiation intercepted by green leaf area (HAA) To explore this alternative, HAA was estimated from leaf area and meteorological data using the same database as in Fig. 2, and the regression of HAA to the obtained grain yield was then analyzed (Fig. 5). For the whole dataset, a linear pattern was observed without any trend to saturate at high values of HAA. According to reduced major axis regression (equation 8), the slope of yield to HAA was 2.08 $g \cdot MJ^{-1}$, which can be considered as the average radiation use efficiency (RUE) during grain filling. Besides, the overall relationship exhibited a positive offset (83 $g \cdot m^{-2}$) suggesting a grain yield could be obtained even if no radiation was intercepted after heading. For each trial, a yield-radiation deviation (YRD) was defined according to equation (9), as the deviation from the yield predicted by HAA. YRD was positive if the yield of a trial was higher than that predicted from its HAA according to equation (8). An ANOVA on YRD values of the protected trials indicated a significant effect of genotype (P <0.01) and environment (P <10^{-3}). As the dataset was unbalanced between genotypes and environments, such an analysis was not taken any further, but YRD in protected trials emerged as a possible index characterizing the response to stress. A second index was set to quantify a HAA-intolerance of cultivars (Int_A) as the ratio of yield loss to HAA loss in unprotected trials (equation 7).

Table 2: Correlations to HAA-indexes, YRD and Int_A, characterizing the profile of cultivar behavior

	Correlation to protected YRD		Correlation to HAA intolerance (Int_A)	
	All data	N-deprivment retired	All data	N-deprivment retired
Protected HAD	-0.35	-0.38 ***	-0.10	-0.10 ns
	ND		ND	
Protected Y	0.48	0.58 ***	0.11	0.09 ns
	ND		ND	
Protected HADE	0.72	0.70 ***	0.21	0.13 ns
	ND		ND	
Protected P	-0.29	-0.39 ***	-0.12	-0.10 ns
	ND		ND	
HAA loss	-0.10	-0.09 ns	0.01	0.02 ns
	ND		ND	
HAD loss	-0.17	-0.15 ns	0.01	0.02 ns
	ND		ND	
Y loss	0.09	0.09 ns	0.39	0.40 ***
	ND		ND	
Total intolerance	0.38	0.31 **	0.85	0.85 ***
	ND		ND	
Specific intolerance	0.12	0.09 ns	0.73	0.80 ***
	ND		ND	

As for Table 1, correlations were calculated either for the whole dataset or discarding 17 trials grown under severe nitrogen deprivement. In the remaining trials, data was normally distributed and the significance of correlations is reported (**:* $P < 10^{-4}$; **: $P < 10^{-3}$; *: $P < 0.01$; ns: $P > 0.05$; ND: not determined).

Table 2 shows the correlations of these two HAA-based indexes to the previous HAD-based indexes characterizing cultivars' behavior. YRD of protected sub-trials correlated negatively to their HAD and yield potential P, and positively to actual yield Y, Int_A, Int_T and especially HADE. Conversely, Int_A highly correlated to both Int_T and Int_S, then it correlated less tightly to yield loss and YRD, but it did not correlate significantly to HAD, Y or P. Interestingly, Int_T and Int_S, Int_A did not correlate to ΔHAD and ΔHAA, which means that tolerances did not correlate to crop susceptibility to disease.

3.7 Profiling the cultivars with either HAD- or HAA-based indexes

Radar plots illustrate profiles of cultivars' behavior of Apache and Charger, as described before (Fig. 6A). As the dataset was unbalanced, it was therefore not adapted to a thorough genotype, environment or *G×E* characterization. Instead, using a balanced sub-dataset, comparison is shown for six cultivars (Fig. 6B) grown under nine environments (site x year combinations). Conversely, the variability of indexes is also shown comparing these environments, each environment value being estimated averaging the previous six genotypes (Fig 6C). High variability was observed for the susceptibility indexes (ΔHAD, ΔHAA), due to variations both in susceptibility to the disease according to cultivars and in the development of the epidemic according to the environments.

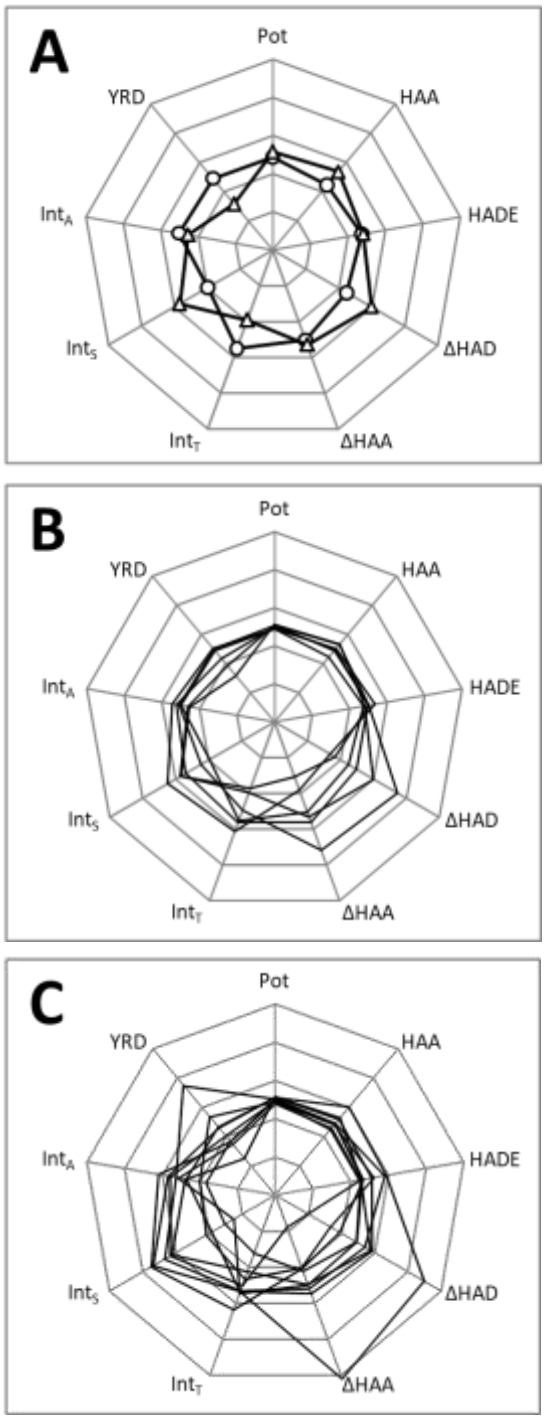

Figure 6: Radar plots illustrating cultivars' behavior of Charger and Apache (6A), a set of six cultivars (6B) and a set of nine environments (6C).
In Fig 6a, symbols are as in figure 1B. Fig 6b and 6c were obtained using a balanced dataset of *six cultivars grown in nine environments (an environment = location x year).*

Conversely, potential yield P, a trait largely worked out by breeders showed very little variability, either between genotypes or between environments. Both HAA and HADE also showed little variability between genotypes, but slightly more between environments. The tolerance indexes (Int_T, Int_S, Int_A and YRD) varied even more, although less than susceptibility, again with a great effect of environment. Tolerance therefore would thus benefit from a *G×E* study.

4. Discussion

4.1 A set of indexes quantifies globally the cultivars' response to stresses

This paper paves the way for a quantitative characterization of cultivars' behavior in large range of environments. Based on well-known relationships between yield and integrated active photosynthetic area (HAD) or cumulative intercepted radiation (HAA) over the grain filling period, a set of indexes was defined that corresponded well to different strategies the genotypes could combine to respond to environmental stresses: susceptibility (ΔHAD, ΔHAA), efficiency (HADE, YRD), tolerances (Int_T ,Int_S, and Int_A). These strategies lead each cultivar to more or less diverge from a potential yield (P) permitted by its HAD, down to its actual yield (Y). Genotype characterization by a set of indexes partly meets the need underlined by Casadebaig *at al.* (2016) to enhance knowledge on the versatility of cultivars released to the market. Close to an ecological characterization of species' responses to environment, i.e. resistance, escape and tolerance in relation to fitness (Ney et al., 2013), it roughly corresponds to productive, ruderal or tolerant types as defined by Grime and Pierce (2012). The originality of this approach was indeed to define and quantify tolerance. In fact, unlike genetic resistance and escape strategies, that both reduce HAD or HAA losses (ΔHAD, ΔHAA), tolerance is not commonly quantified or often confused with them. Thus, the proposed characterization of cultivars by a global approach constitutes a first step towards an identification of main traits involved in each adaptive strategy to combine them at best to attenuate impacts of stress.

The previous set of indexes was calculated for each G×E situation, but using an unbalanced dataset combining contrasted situations of septoria severity and varieties. As a first approximation, and because we focused on the development of a set of indexes characterizing the genotypes, trait analysis was based on the raw OLS or RMA correlations between the traits although the data are neither strictly independent nor randomly distributed. To overcome these difficulties often met when using composite datasets, Piepho (2018) proposed a nice bivariate analysis framework decomposing the impacts of treatments and experimental designs on correlations. More in-depth knowledge of the characteristic traits of varieties will greatly benefit from such approach. It is nevertheless quite data intensive and better suited to specifically designed datasets. Therefore, it was not achieved in this paper that mainly focused on the building of indices.

4.2 No trade-off between productivity and total tolerance allows breeding for both to face stresses

Subject to the precautions mentioned above, this quantitative characterization of cultivars allowed checking the potential trade-off between indexes, i.e. breeding strategies. A major obstacle to the use of tolerance by breeders was thus removed. Without any doubt, no negative trade-off related total tolerance (Int_T) to actual yield in protected trials (Y). Tolerance is thus not restricted to low yielding crops, but also suitable for selection of elite lines. Potential yield (P), the maximum yield observed at a given HAD even increased total tolerance (Int_T) of crops, somewhat explaining why these strategies were selected together by breeders. Contrarily, specific tolerance (Int_S), i.e. tolerance left once HAD impact on total tolerance Int_T was withdrawn, correlated negatively to both Y and P. In the present dataset, this trade-off was counterbalanced because Y positively correlated with HAD. In other words, the trials showing the best Y also had a higher HAD that compensated their increase in specific intolerance (Int_S). Breeding might not support such a trend to increase HAD however, because another unfavorable trade-off showed up from dataset: the higher the potential yield, i.e. the higher the protected HAD, the higher the susceptibility to septoria (HAD), with a highly significant correlation. Breeders could dispute this point; indeed newly released cultivars generally exhibit both high HAD and low susceptibility, thanks to the use of new resistance alleles. Yet the sustainability of such a strategy is questionable, as HAD increased crop susceptibility, probably by causing crop microclimates that favor disease development (Calonnec et al., 2013). Therefore, despite HAD positively correlated to yield potential (P) and favored tolerance, breeding for higher HADs should be cautiously recommended. Alternatively, despite Int_S being laborious to quantify (see below), its trade-off with yield needs thorough studies for a use in plant breeding. However, the large scattering of points observed in trade-off fortunately suggests that cultivars with both high yield and specific tolerance may exist; such as varieties with increased HAD efficiency (HADE), for example. In our dataset finally, no trade-off between both total or specific tolerance and susceptibility to diseases was found, in line with ecological studies showing mixed strategies of defense occur in natural ecosystems (Carmona and Fornoni, 2013). Higher yields neither resulted in an increase in disease susceptibility, as no correlation was observed between Y of protected trials and losses of either HAD, or yield by unprotected trials. Breeding for high yield cultivars that are both resistant and tolerant to Septoria is thus achievable.

4.3 HAD-indexes however strongly depend on the setting of the reference potential curve

The curvilinear relation of HAD to P is likely an effect of the saturated light absorption in dense canopies (Monteith and Moss, 1977). This therefore questions the use of Int_T to characterize tolerance: Int_T changes with HAD values, while HAD shows a large variability that is difficult to manage due to its complex *G×E* determinism. Additionally, as disease epidemics and therefore the corresponding HAD losses are highly variable, Int_T largely varies from a trial to another (Collin et al, 2018), making difficult the comparison between trials. Defining Int_S was thus an attempt to account for the part of tolerance independent of HAD variations. Unfortunately, Int_S calculation needed the establishment of a potential curve as a reference, which presents in it-self two main drawbacks. Firstly, the reference curve is purely empirical; its adjustment by quantile regression could move according to its parameterization and the threshold chosen to fix the boundary line. Secondly, equation (1) was fitted to a given dataset, but its adequacy had not been evaluated using an independent dataset; its universality could therefore be challenged for growing conditions far from those of France. The resulting bias could affect the straight genetic dependence of Int_S that needs thus thorough investigation *per se*. Nevertheless, our procedure allowed pointing out that the total tolerance of high yielding cultivars is too much linked to the extent of their canopy. The use of the reference curve made it possible to detect a trade-off between yield and specific tolerance which, otherwise could accumulate silently in the new cultivars. Furthermore, it suggested that agricultural practice (e.g. fertilization) affect this trade-off. Correlations between indexes pointed out which cultivars' strategies may coexist and which require a specific attention by breeders to limit their drawbacks.

4.4 An easy-to-use tool provided to breeders: towards indexes based on proxies

So far HAD and therefore, tolerance, have not been taken into account in the evaluation of cultivars, as their calculation needed repetitive green area measurements during grain filling. High throughput phenotyping tools hold the promise to give access to a large amount of crop variables at various time and space scales using proxies (Christopher et al., 2014; Comar et al., 2012). Moreover, remote sensing already gives access quite directly to light interception, without making hypotheses on crop architecture, leaf and non-leaf green organs and so on. Then developing indexes based on HAA rather than on HAD could open an opportunity for breeders to characterize genotypes through new kinds of indexes. In this paper, HAA was calculated using a common 0.68 coefficient for light interception in equation (6), neglecting it could change between

both genotype and crop management (Costes et al., 2013), while such change had be pointed out as a possible source of tolerance (Bingham and Topp, 2009). Although not allowing a precise comparison of cultivars, this approximation was a first step in constructing indices based on HAA. As for HAD-based indexes, genetic and *G×E* effects could be taken into account by estimating their distance to a common trend, here an overall regression line (Bogard et al., 2010). To increase the precision in assessment in this common trend, we used a reduced major axis regression (RMA) instead of the ordinary least square method (OLS; Smith, 2009). Compared to OLS regression, RMA regression commonly decreases the offset, which remained positive. The offset between HAA and yield was previously interpreted as the mobilization of early-accumulated carbohydrates to sustain grain growth independently of photosynthesis (Bancal et al., 2007). The YRD index could capture the variability of carbohydrate reserves between trials, although this remains to demonstrate. In our dataset, YRD positively correlated to Y and Int_T. Reserve mobilization is intuitively a way to maintain yield by compensation for photosynthesis shortage when disease decreases the green area (Parker et al., 2004). In that meaning, the high correlation of YRD to HADE makes sense: buffering grain nutrition with climatic variations, reserves would increase HAD efficiency. Therefore, the negative effect of YRD on tolerance was somewhat surprising, but Foulkes et al. (2006) already observed a positive correlation of stored carbohydrate to Int_T. Perhaps is it driven by the negative correlation of YRD to HAD, i.e. carbohydrate storage leading to weaker HAD, a process that should be studied in more detail.

The second HAA-based index, HAA-intolerance or Int_A, combined reserve consumption and possible RUE variation induced by stressful conditions. It was highly correlated to both Int_T and Int_S, but not to potential or actual yields, regardless of fertilizer management. HAA-intolerance directly correlated to yield loss, and it could therefore be a simpler breeding tool than HAD-based intolerance indexes, if direct HAA measurements become easily available.

4.5 Conclusion and perspectives

Crops may mobilize different strategies to limit impacts of stress. The present framework proposed to quantify them altogether using a panel of HAD-based indexes; it was then applied to a dataset regarding several cultivars under a range of environments. Simpler HAA-based indexes were also evaluated, as opening the way to an easy and global characterization of cultivars by breeders. No trade-off showed up between tolerance and potential yield or between tolerance and susceptibility. The chosen indexes showed a variability not only driven by genotype. Instead, indexes varied even more between the environments than between the cultivars, as previously found for yield (Casadebeig et al, 2016). If these indexes may be used to profile ecological behavior of cultivars, they also may characterize environments where specific traits as potential yield, efficiency, susceptibility or tolerance may better express. However, large and balanced databases are necessary to properly analyze and predict how to fit genotypes to environments at best. This study opens this perspective especially with the development of HAA-based indexes.

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