Interpreting QTL x environment interaction and QTL specificity to environments for kernel number in winter wheat with an environmental characterization based on probe genotypes

Martine Leflon[1], Anne Laperche[2], Wen-Ying Rong[2], Jacques Le Gouis[2], Christophe Lecomte[3], Beghin Denis[2] and **Maryse Brancourt-Hulmel[2]**

[1] INRA, Unit? de G?n?tique et d'Am?lioration des Plantes 35650 Le Rheu FRANCE www.inra.fr Email leflon@rennes.inra.fr
[2] INRA, BP 136 Estr?es-Mons 80203 PERONNE C?dex FRANCE www.inra.fr Email brancour@mons.inra.fr
[3] INRA, Station de G?n?tique et d'Am?lioration des Plantes, 17 rue Sully, BP 86510, 21065 Dijon C?dex FRANCE www.inra.fr Email lecomte@epoisses.inra.fr

Abstract

Environmental characterization has been shown to aid interpretation of genotype environment interaction. In this study, we present a novel method to characterize environments and its use to explain specificity of QTLs to environments. The study examines variation in kernel number in a wheat double haploid population. The environmental characterization method is based on the use of a simple yield components relationship between maximal thousand kernel weight and kernel number per square meter for each of four probe genotypes. Deviations from thresholds defined in the relationship are used to identify environmental indicators related to yield limitation in the test environments. The environmental indicators are used to partition the QTL x environment interaction and to explain the specificity of some QTLs to some environments using a four-step strategy.

Media summary

An environmental characterization based on probe genotypes helps to explain QTL environment interaction and QTL specificity to environments for kernel number in winter wheat.

Key Words

Environmental characterization, QTL x environment interaction, QTL specificity, kernel number, winter wheat

Introduction

Environmental characterization has been shown to aid interpretation of genotype x environment interaction (Chapman et al, 2003). Interpretation of QTL x environment interaction (QEI) could also benefit from environmental characterization. Our objective in this study was to characterize the growing environment of winter wheat to better understand QTL x environment interaction found in multi-environment trials and to explain the specificity of QTLs to some environments. We characterized the environment using yield component responses of a small set of probe genotypes. Responses were quantified using deviations from a yield component relationship between maximal thousand kernel weight and kernel number per square meter (KN). Associations of these deviations with a set of environmental attributes underpinned the environmental characterization. Using the test variable, KN, we show how this characterization of environments can be used to explain QTL x environment interaction and QTL specificity to some environments.

Methods

Four probe genotypes (Arche, Ritmo, Soissons, and R?cital) and a population of 220 double haploid lines derived from the cross between the parents "Arche" and "R?cital" were studied in three locations in France (Mons, Le Moulon, Clermont-Ferrand), over two years (2000 and 2001) and under two nitrogen levels (low (N-) and high (N+)). Meteorological data and the kernel number were measured, as well as

other agronomic and biological traits. Maximal TKW, KN threshold, and potential grain yield of the simple yield component relationship were obtained by boot-strapping (as done by Brancourt-Hulmel et al. 1999). QTL analysis was performed using an existing genetic map from a G?noplante project and the computer program PLABQTL (Utz and Melchinger 2000).

Results

Part I: Characterization of environments

The characterization of environments is based on observation of a specific set of three to four probe genotypes. The probe genotypes must fulfil the following requirements: their reactions to environmental factors are known; their sensitivities to yield-limiting factors are complementary; their earliness and interaction pattern are complementary (Brancourt-Hulmel et al. 2001). The probe genotypes in our experiment were Arche, R?cital, Soissons, and Ritmo. For each probe genotype in each environment, a kernel number (KN) deviation was determined (figure 1) as the difference of the kernel number threshold from the observed kernel number, expressed as a % of the threshold value. The threshold value represented the value for the genotype in an environment free from stress. When KN deviation is negative (ie. KN < KN threshold), environments were imposing constraints (Brancourt-Hulmel et al. 2000).

Subsequently, the potentially limiting environmental constraints were then identified and assessed. 109 environmental indicators related to temperature, radiation, water deficit and biological indicators (including nitrogen bio-indicators) were determined for the probe genotypes. The indicators were selected in three steps. A first selection was done by principal component analysis (PCA) where all meteorological or plant measured indicators (ie. bio-indicators) were introduced. Only the 38 indicators strongly correlated to the PCA axes were retained. The second round of selection was done via another PCA that was conducted on the four families corresponding to measures of temperature, radiation, water deficit or plant attributes. This second round was required to select a minimum of indicators in each family. In this case, 40 indicators were selected. In the final step, pairwise correlations between the indicators selected by the two methods, were calculated. If a correlation exceeded 80%, the corresponding indicator was kept. This resulted in 16 temperature, 11 radiation, 10 water-deficit, and 7 bio-indicators being retained for a total of 44 indicators. 44 indicators for each of four probe genotypes resulted in 176 environmental variates. Then a multiple linear regression was carried out to relate kernel number deviation (as done by Leflon et al. in press) with variates selected from the 176 environmental variates.

Part II: Partitioning of QEI and explaining QTL specificity to environments.

The strategy used consisted in:

1. detecting QTLs for KN.

2. detecting QTLs for the traits defined as sensitivity to the different environmental covariates (ie. “environmental sensitivity QTLs”). The sensitivity is estimated using the slopes from the factorial regression (Denis 1988).

3. studying the co-localisations of the QTLs detected in both ways and, in the case of a co-localisation, partitioning the QEI using the co-located covariates.

4. describing the environments where QTLs were detected for KN using the co-located covariates.

The QTL found on chromosome 1B (Table 1) was related to “water deficit from spike at 1 cm to meiosis measured for Soissons” (spetpemS), “nitrogen nutrition index measured at flowering for Arche” (finnA), and the “sum of daily radiation from meiosis to flowering measured for Arche” (srglmfA). The QTL found on chromosome 2D was related to the covariates spetpemS, finnA, srglmfA, and the “sum of high temperature above 25?C -3/+3 days at meiosis measured for Arche” (stcmbA). The QTL found on chromosome 3 D was associated with the “sum of high temperature above 25?C from heading to

flowering measured for Soissons" (st25efS). One of the four QTLs found on chromosome 4B was associated with the "nitrogen nutrition index" measured at flowering for all the probe genotypes: R?cital (finnR), Ritmo (finnI), Arche (finnA), and Soissons (finnS). The second QTL on this chromosome was associated with the "sum of high temperature above 25?C -3/+3 days at meiosis measured for Ritmo" (stcmbI). The third QTL was associated with the "sum of daily radiation -3/+3 days at meiosis measured for Arche" (srglmbA) and the last QTL with the "sum of daily temperature above 25?C from heading to flowering measured for R?cital" (st25efR).

Environments where QTLs were detected for KN can be described by the previous co-located covariates which partitioned each QTL (covariates data not shown).

- QTL 1B was found only at Mons in 2000 at N+ nitrogen level. This environment was limited by early water deficit, nitrogen stress at flowering, and radiation from meiosis to flowering.
- QTL 2D was found in four environments: at Mons in 2000 at both levels, at Clermont in 2001 at N+, and at Le Moulon in 2001 at N-. At Mons in 2000 at N-, there was nitrogen stress (finnA) but also high stress of high temperature around meiosis (stcmbA). At Mons in 2000 at N+, there was a low nitrogen stress (finnA) and a high stress of high temperature around meiosis (stcmbA). At Clermont in 2000 at N-, there was no nitrogen stress (finnA) but water deficit from spike at 1cm to meiosis (spetpemS). At Le Moulon in 2001 at N-, spetpemS, finnA, and srglmfA indicated that several stress occurred at a high intensity.
- QTL 3D was found at Mons in 2000 and at Clermont in 2001 at both nitrogen levels. It was not associated with a nitrogen effect but probably with a slight effect of high temperature during the heading (st25efS): at Mons in 2000 at N-, there was effect of high temperatures whereas no effect was found at Mons in 2000 at N+ and at Clermont in 2001 at both levels.
- QTL 4B(1) was found in five environments: at Clermont in 2000 at N+, at Le Moulon in 2000 at both nitrogen levels, at Mons in 2000 at N+ and at Le Moulon in 2001 at N-. At Clermont and Le Moulon in 2000 at N+, no nitrogen stress was recorded; finnR, finnI, finnA, and finnS showing very small values. At Mons in 2000 at N+, nitrogen stress was not completely avoided; finnR, finnI, and finnA showing intermediate values. The nitrogen stress at Le Moulon in 2000 N- was globally very high (very high values for finnI and finnA, high values for finnR and finnS). Nitrogen stress was variable at Le Moulon in 2001 at N- (no stress shown by finnR and finnS, moderate stress by finnI, and high stress by finnA).
- QTL 4B(2) was found in environment Le Moulon in 2001 at N-. There was no effect of high temperature at meiosis in this environment.
- QTL 4B(3) was detected at Clermont in 2001 at N- where radiation at meiosis limited KN.
- QTL 4B(4) was found at Mons in 2000 at N-. This environment was subjected to a high effect of high temperature from heading to flowering.

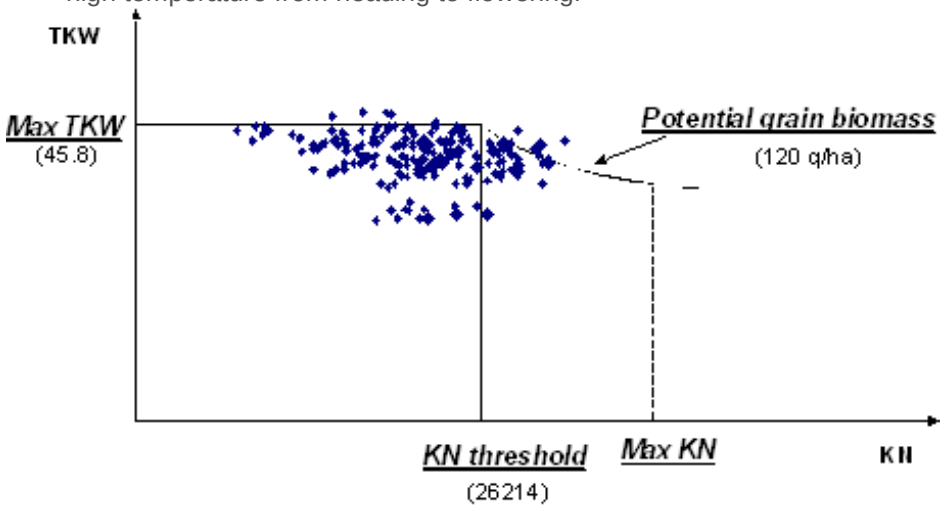

Figure 1. Boundary curve determined for the relationship between TKW and KN (cultivar Arche).

Table 1. QEI partitioning with the environmental covariates. Codes of the covariates are given in the text.

QTL	Covariate	Explained sum of squares (in %)	Cumulated explained sum of squares (in %)
QTL 1B	spetpemS	49	
	finnA	12	
	srglmfA	10	71
QTL 2D	spetpemS	64	
	finnA	7	
	srglmfA	4	
	stcmbA	5	80
QTL 3D	st25efS	53	53
QTL 4B (1)	finnR	32	
	finnI	32	
	finnA	13	
	finnS	4	81
QTL 4B (2)	stcmbI	16	16
QTL 4B (3)	srglmbA	21	21
QTL 4B (4)	st25efR	15	15

Conclusion

The selected covariates based on environmental attributes associated with probe genotypes and a simple yield component relationship enabled detection of environmental covariates that limited the formation of KN and that partitioned QEI. The environmental covariates corresponded to indicators related to temperature, radiation, water-deficit, as well as bio-indicators. An improvement of the method could be to select the covariates for their contribution to the genotype x environment interaction instead of their contribution to the environmental main effect (Brancourt-Hulmel et al., 2000). The method used enables explanation of why some QTLs detected for KN are only detected in some environments. This approach might be usefully linked with recent advances in crop modelling (Chapman et al. 2003).

References

Brancourt-Hulmel M, Lecomte C and Meynard JM. (1999). A diagnosis of yield-limiting factors on probe genotypes for characterizing environment in winter wheat trials. Crop science 39, 1798-1808.

Brancourt-Hulmel M, Lecomte C and Denis JB (2001). Choosing probe genotypes for the analysis of genotype x environment interaction in winter wheat trials. Theoretical and Applied Genetics 103, 371-382.

Brancourt-Hulmel M, Denis JB and Lecomte C (2000). Determining environmental covariates which explain genotype x environment interaction in winter wheat through probe genotypes and biadditive factorial regression. Theoretical and Applied Genetics 100, 285-298.

Chapman S, Cooper M, Podlich D and Hammer G (2003). Evaluating plant breeding strategies by simulating gene action and Dryland environment effects. Agronomy Journal 95, 99-113.

Denis JB (1988). Two way analysis using covariates. Statistics. 19, 123-132.

Leflon M, Lecomte C, Barbottin A, Jeuffroy MH, Robert N and Brancourt-Hulmel M (in press). Characterization of environments and genotypes for analyzing genotype x environment interaction: some recent advances in winter wheat and prospects for QTL detection.

Utz HF and Melchinger AE (2000). A computer program to map QTL. University of Hohenheim. D-70593 Stuttgart Germany.