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Research Article

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Marker Association Analysis with Three Agronomic Traits in Hard Winter Wheat Lines under Diverse Environments

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Abstract

Genetic performance for a quantitative trait is often controlled by gene-by-gene and genotype-by-environment (GE) interaction effects. As an important component, a GE interaction effect is highly related to crop stability. As genetic association mapping has been widely used to determine markers associated with traits of interest, stability analysis based on genetic markers/genes of importance could help develop widely adapted or specifically adapted cultivars. With linear mixed model approach, in this study we analyzed a wheat data set from the USDA Hard Winter Wheat Regional Nursery Program in 2010. The data included 32 genetic markers and 48 genotypes with three important agronomic traits: grain yield, plant height, and heading date, which were measured under multi-environments. Our results showed that four important DNA markers: Rht2, PPO18NED, Lr34JagTM, and Waxy-A1-AFC-AR2FAM, were significantly associated with all these three traits. Among these, Rht2 contributed 50.34%, 78.65% and 53.90% of the phenotypic variation for grain yield, plant height and heading date, respectively. Compared to their main effects, however, genotype-by-environment interaction effects were less important under these diverse environments.

Keywords

Gene expression; Winter wheat; Genetic marker; Agronomic trait

Introduction

Wheat, as an important source of protein, vitamins and minerals [1], is a major consumed food crop around the world. The world production of wheat in 2012 was 670 million metric tons, making it the second most-produced cereal after rice (719 million metric tons) [2]. Wheat feeds 4.5 billion people in 95 developing countries [3]. As the population continues to increase, genetic improvement in wheat yield, quality, and resistance is more urgent to meet such a great need.

Association mapping has been widely used in detecting genetic markers associated with traits of importance that can be used for crop/animal improvement [4-9]. Various useful statistical methods and computing tools have been developed to meet such a great need for association mapping studies [10-21]. These methods have been applied to various plant species, including wheat [22-27], barley [28-31], rice [32-35] soybean [36-38] and cotton [39,40]. However, many association mapping studies were focused on studies under single or a few environments. For example, the numbers of environments used for many wheat association mapping were normally fewer than five [41,42] yet only a few studies used a little large number of environments for association mapping in wheat [43].

The Hard Winter Wheat Regional Nursery (HWWRN) Program, coordinated by U.S. Department of Agriculture - Agricultural Research Service (USDA-ARS), aims to evaluate various advanced breeding lines and commercial winter wheat cultivars in multi-state environments. More importantly, these winter wheat genotypes have been genotyped with various DNA markers with potentially known gene functions. For example, the major dwarfing genes like Rht1 andRht2, which could reduce plant height by reducing the response to gibberellin with pleiotropic effects on grain number and yield [43,44] were used to genotype 48 winter wheat lines in 2010. Various DNA markers linked to important genes in hard winter wheat were reviewed in a recent publication [45]. Such resources could provide a great opportunity for both yield stability analysis for each winter wheat cultivar, but also for determination of DNA marker associations with traits of interest under a wide range of growing environments. Appropriate genetic data analysis should provide useful genetic information to determine appropriate winter wheat cultivars. With such wheat data under multi-environments, various genetic models can be employed to reveal rich genetic information that can be used for winter wheat line selection.

In this study, we focused on analysis of HWWRN data collected by 20 institutes in 2010. The data included three important agronomic traits: grain yield, plant height, and heading date measured under diverse environments and 32 genetic markers for 48 winter wheat cultivars. First we used a one-way ANOVA model to determine each of these DNA markers associated with traits of interest under different environments. Secondly, we applied a linear mixed model approach to investigate the contributions of several these markers associated with these three agronomic traits across environments. The main objective of this study was to determine the stability of these gene expressions under various environments and provide information to select superior genotypes with stable performance.

Materials and Methods

Materials and experiments

The nursery program includes the Southern Regional Performance Nursery (SRPN), the Northern Regional Performance Nursery (NRPN) and the Regional Germplasm Observation Nursery (RGON). The winter wheat phenotypic and genotypic data were downloaded from the Hard Winter Wheat Regional Nursery Program of U.S. Department of Agriculture, which conducted by 20 institutions in 2010. We only used the phenotypic and genotypic data from SRPN in this study. Three agronomic traits, grain yield, plant height, and heading date, were available in 30, 18 and 13 environments (Table 1) and used in this study. Forty-eight winter wheat lines were screened with 38 genes/markers. Six markers were removed due to their monomorphism and nine genotypes were removed from the data set due to missing markers. Therefore, the data used in this study

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contained 39 genotypes and 32 DNA polymorphic genes markers (10 dominant and 22 co-dominants) (Table 2).

Genetic models

Due to the winter wheat data structure, several different models such as stability analysis and gene expression analysis under different environments can be used for analyzing multi-environmental data. In this study, we emphasized two genetic models. The first genetic model is described as follows.

For a particular marker, there could be all homozygous and heterozygous combinations like AA, BB, and/or AB among 39 cultivars. Therefore, the model 1 actually is a one-way ANOVA model for each marker, where g could be different for different markers:

$$y_{ij} = \mu + G_i + e_{ij} (i = 1,2,...,g; j = 1,2,...,n_i) \quad (1)$$

where y_{ij} is the phenotypic value for the marker with genotype i; n_i is the total number of for genotype i; and $e_{ij} \sim N(0,\sigma_e^2)$ is a random error.

On the other hand, gene expression for each of these traits under these environments could be controlled by genotype-by-environment (GE) interaction. Investigation of GE interactions at DNA marker level is helpful to select cultivars adapted to diverse environments with specific markers. Therefore, we also analyzed each marker including its GE interactions with the following linear mixed model.

Table 1: Winter wheat agronomic traits among different environments in the Hard Winter Wheat Southern Regional Performance Nursery Program of U.S. Department of Agriculture in 2010.

Environment	Abbreviation	Grain yield	Plant height	Heading date
Clovis, NM dryland	E1	×†	×	×
Clovis, NM irr.	E2	×	×	×
Farmington, NM irr.	E3	×	×	×
Bushland, TX dryland	E4	×	×	×
Bushland, TX irr.	E5	×	×	×
Chillicothe, TX	E6	×		
Prosper, TX	E7	×		
Stillwater, OK	E8	×		
Goodwell, OK irr.	E9	×		
Lahoma, OK	E10	×		
Granite, OK	E11	×		
Akron, CO	E12	×	×	×
Burlington, CO	E13	×		
Fort Collins, CO irr.	E14	×	×	×
Washington, CO	E15	×	×	
Hays, KS	E16	×	×	×
Hutchinson, KS	E17	×		
Salina, KS	E18	×		
Colby, KS	E19	×	×	×
Garden City, KS	E20	×	×	×
Wichita, KS	E21	×	×	×
Winfield, KS	E22	×		
Lincoln, NE	E23	×	×	×
Clay Center, NE	E24	×	×	
North Platte, NE	E25	×	×	
Sidney, NE	E26	×	×	
Alliance, NE	E27	×	×	
Brookings, SD	E28	×		
Dakota Lakes, SD	E29	×		
Pine Bluffs, WY	E30	×	×	×

†: X indicates a trait being measured under that environment

Table 2: DNA marker information.

DNA Marker	Marker Number	Type
WMC0331NED	1	Co-dominant
Rht1	2	Dominant
Rht2	3	Dominant
GWM0261NED	4	Co-dominant
SNP8-FHB	5	Co-dominant
UMN10VIC	6	Co-dominant
Lr19-130NED	7	Dominant
Lr19-DomNED	8	Dominant
csLV34-Lr34FAM	9	Co-dominant
Lr34TM	10	Co-dominant
Lr34JagTM	11	Co-dominant
Lr34	12	Co-dominant
VentriupLn2PET	13	Dominant
Sr2-STM559TGAGNED	14	Co-dominant
Sr2-X3B028F08PET	15	Dominant
Sr24#50FAM	16	Dominant
Sr25-BF145935VIC	17	Co-dominant
PPD-D1,R1,R2VIC	18	Co-dominant
BAR0012FAM	19	Co-dominant
BAR0170VIC	20	Co-dominant
CDO708FAM	21	Co-dominant
VRN-A1-SNPF	22	Co-dominant
VRN-D3-F6R8NED	23	Co-dominant
TSM0120FAM	24	Dominant
UMN19(GluA1)NED	25	Co-dominant
BxMARFAM	26	Co-dominant
UMN25(GluD1)NED	27	Co-dominant
UMN26(GluD1)PET	28	Co-dominant
PPO18NED	29	Co-dominant
PPO29NED	30	Dominant
Waxy-A1-AFC-AR2FAM	31	Co-dominant
GWM0469VIC	32	Dominant

$$y_{hij} = \mu + E_h + G_i + GE_{hi} + e_{hij} (h = 1,2,...,l; i = 1,2,...,g; j = 1,2...,n_i) \quad (2)$$

Where E_h is an environmental effect; G_i is a genotypic effect for a marker and GE_{hi} is a GE effect for a marker and environment interaction; and e_{hij} is a random error.

Statistical methods

With model (1), an analysis of variance (ANOVA) method was employed and adjusted coefficient of determination (R^2) was estimated for each DNA marker under each environment. For model (2), a minimum norm quadratic unbiased estimation (MINQUE) was applied to estimate all variance components with 10-fold jackknife technique applied [46-48]. All data analyses were implemented by R computer language (Version 3.0.1) [49] and with an R package "minque' [46].

Results and Discussion

Single environment analysis for three agronomic traits

First, each marker under each environment was analyzed separately with model (1). The corresponding contribution (represented by an adjusted coefficient of determination, defined as R^2) to the phenotypic variation for each of three agronomic traits was estimated. The results are provided in Figure 1.

DNA marker 2 (Rht1) made consistently higher contribution to three wheat traits than the other markers (Figure 1), indicating that Rht1 was highly associated with wheat traits grain yield, plant height, and heading date under these environments. The contribution of from this DNA marker to grain yield ranged considerably from 0.88 to 55.02% among 32 environments. As for plant height, the range of contribution was 14.81 to 71.24% among 18 environments, while for heading date, the contribution ranged from 1.05 to 38.10% among 13 environments. Rht1 was widely reported as a DNA marker related to plant anatomy and morphology, especially plant height [44,50]. The marker, VRN-D3-F6R8NED, is related to a vernalization gene and has an impact on development at stem elongation, heading date, and physiological maturity [51].

DNA marker 23, VRN-D3-F6R8NED, was highly associated with heading date (Figure 1). The contribution for VRN-D3-F6R8NED ranged from 2.18 to 32.24% for heading date among different environments. The wide ranges of genetic association with these three agronomic traits for these markers suggested that the expression of these markers under different environments varied and utilization of these markers should be environment-specific.

Single marker association analysis with three traits across environments

Each of these 32 markers was analyzed subject to *Model 2* to investigate the GE interaction effects. The variance components for genotypic and GE interaction effects expressed as proportional variance components were estimated by a MINQUE approach and results are summarized in Table 3. Most markers showed small or no significant contributions to these three agronomic traits. Genotypic effects for marker Rht1 accounted for 50.34, 78.65 and 53.9% of total variations for grain yield, plant height and heading date, respectively. Genotypic effects for markers Lr34JagTM and Lr34 showed significant contributions to plant height (44.5% and 27.0%, respectively). Genotypic effects for PPO18NED had a major contribution (46.9%) to grain yield while no significant contributions to the other two traits. Genotypic effects for TSM0120FAM contributed 18.8% and 28.9% of total variations to plant height and heading date, respectively. Waxy-A1-AFC-AR2FAM contributed 13.5 and 43.0% to plant height and heading date with genotypic effects. On summary, four markers, seven markers, and nine markers made greater than 10% contribution to grain yield, plant height, and heading date, respectively. Among these markers with major contributions to these three traits, marker Rht1 showed major pleiotropic effects on all three traits. The results were in agreement with other studies [50,52,53].

Compared to genotypic effects, GE effects for these markers made small or insignificant contributions to the three traits. Among these markers only markers Rht1 and GWM0261NED had significant GE effects for grain yield (Table 3), suggesting that yield stability for these winter wheat cultivars were not related with genetic expressions of these markers and other markers or genes may be responsible for yield stability for these cultivars.

Conclusion

In this study, two different models were employed to identify desirable DNA markers with high performance stability in winter wheat cultivars. The first model was a single marker model under each environment and the second one with GE effects included. The results obtained by both methods were comparable. Markers with major contributions to these three traits were identified by both models;

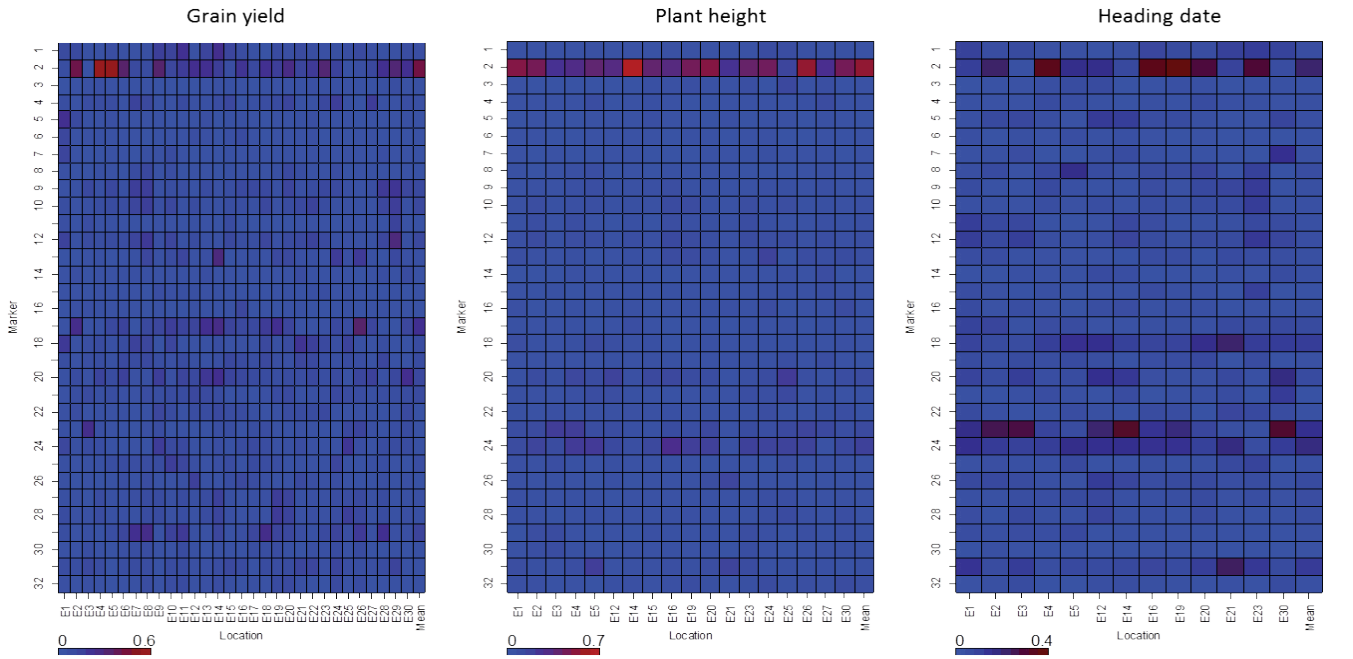

Figure 1: The contribution (coefficient of determination R^2) of each marker to three wheat traits (grain yield, bu/ac; plant height, in; and heading date, days) under different environments in Model 1 (Abbreviation for locations and markers can be found in Tables 1 and 2).

Table 3: The proportional variance components of genotypic effects (V_G/V_P) and genotype-by-environment interaction effects (V_{GE}/V_P) for three wheat traits subject to Model 3.

	Grain yield		**Plant height**		**Heading date**	
Marker #	V_G/V_P	V_{GE}/V_P	V_G/V_P	V_{GE}/V_P	V_G/V_P	V_{GE}/V_P
1	0.020*	0.000	0.005	0.000	0.044*	0.000
2	**0.503****	0.147**	**0.787****	0.027	**0.539****	0.069
3	0.059**	0.000	0.020	0.000	0.077	0.000
4	0.051**	0.081*	0.019	0.000	0.084*	0.000
5	0.011	0.000	0.000	0.000	0.084*	0.000
6	0.008	0.000	0.037	0.000	0.069	0.000
7	0.045	0.000	0.017	0.000	0.096**	0.000
8	0.004	0.000	0.007	0.000	0.117**	0.000
9	0.052**	0.000	0.007	0.000	0.010	0.000
10	0.054**	0.000	0.036	0.000	0.017	0.000
11	0.021	0.000	**0.445****	0.000	0.121	0.000
12	0.034**	0.000	**0.270****	0.000	0.047	0.000
13	0.017*	0.010	0.073**	0.000	0.009	0.000
14	0.003	0.004	0.006	0.000	0.043	0.000
15	0.001	0.000	0.017	0.000	0.010	0.000
16	0.007	0.000	0.021*	0.000	0.007	0.000
17	0.118**	0.000	0.001	0.000	0.021	0.000
18	0.028*	0.000	0.009	0.000	0.150**	0.000
19	0.126**	0.000	0.000	0.000	0.048	0.000
20	0.066**	0.000	0.214**	0.000	0.149*	0.000
21	0.040**	0.000	0.013	0.000	0.003	0.000
22	0.001	0.000	0.040**	0.000	0.002	0.000
23	0.002	0.000	0.079**	0.000	0.221*	0.000
24	0.003	0.000	0.188**	0.000	**0.289****	0.011
25	0.021*	0.000	0.003	0.000	0.024	0.000
26	0.037	0.000	0.044	0.000	0.201	0.000
27	0.005	0.000	0.011	0.000	0.091*	0.000

28	0.021	0.000	0.036*	0.000	0.101**	0.000
29	**0.469****	0.000	0.131	0.000	0.030	0.000
30	0.019*	0.000	0.032	0.000	0.000	0.000
31	0.014	0.000	0.135**	0.000	**0.430****	0.000
32	0.009	0.000	0.087**	0.000	0.005	0.000

V_G=Genotypic variance component due to marker effects; V_{GE}=Variance component due to marker and environment interaction effects; and V_P=Phenotypic variance

however, GE interactions for these markers under these diverse environments were very small (Figure 1 and Table 3). DNA marker ***Rht1*** on the short arm of chromosome 4B [54] was significantly detected for all three traits. This DNA marker was reported to be associated with plant anatomy and morphology [55,56]. Rht1 was also reported to be associated with Septoria tritici blotch [57]. It appears that Rht1 shows pleiotropic effects [58-61]. We also detected that the DNA marker ***VRN-D3****-F6R8NED* was highly associated with heading date [51]. The marker *VRN-D3-F6R8NED* is a vernalization gene, which controls heading date [51]. With the application of linear mixed model-based association mapping, in addition to DNA marker *Rht1*, DNA markers *PPO18NED* is associated with grain yield [62], *Lr34JagTM* is a wheat leaf rust resistance gene and was reported to be associated with plant growth and grain yield in Barley [63,64]. We found the similar result that this marker was significantly associated with plant height. *Waxy-A1-AFC-AR2FAM*, a co-dominant marker located on chromosome 8AS, was significantly associated with for heading date. Our results showed that the expression levels of the DNA marker *Rht1* varied among different environments by single marker model and were confirmed by Model 2 as well.

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