

Molecular genetic mapping of quantitative trait loci associated with loaf volume in hexaploid wheat (*Triticum aestivum*)

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Abstract

Major efforts in wheat research are being made to improve the yield and quality of wheat. Loaf volume (Lv) is the main quality parameter deciding the bread making potential of wheat. To genetically dissect quantitative trait loci (QTLs) for Lv, a Recombinant Inbred Line (RIL) population (F₈) was developed from a cross between two Indian wheat varieties “HI 977” and “HD 2329”. A total of 914 SSR and 100 ISSR primers were used for molecular analysis and the genetic map comprising 19 chromosomes was constructed with 202 SSR markers and 2 HMW glutenin subunit loci: Glu-B1 and Glu-D1. The phenotypic data were collected from six environments including three different agro-climatic zones for 2 consecutive years. Dissection of Lv through AMMI model revealed significant G × E variance for the trait. QTL analysis was performed using composite interval mapping. A total of 30 QTLs for Lv were detected and significant QTLs were identified on 6B and 6D chromosomes; 1B, 1D, 2A, 3A, 5B and 5D also contributed genetically to Lv. Association between 6B and 6D QTLs and variable expression of gliadins on group 6 chromosomes were discussed. QTLs detected in this study were compared with other QTL analysis in wheat.

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1. Introduction

Bread making quality (BMQ) of wheat is considered to be a complex trait influenced by interactions of many biochemical traits such as seed protein quality and content (Payne et al., 1987), starch quality and content (Gray and Bemiller, 2003) and oil content (Helmerich and Koehler, 2005) supplemented by various physico-chemical traits such as moisture content, water retention capacity, vacuole formation, grain hardness and texture (Huang et al., 2006).

Considerable studies have been accomplished in BMQ during the last two decades. Payne et al. (1987) and Garcia-Olmedo et al. (1982) evaluated some of the alleles at the high-molecular-weight (HMW) glutenin subunit loci

(*Glu-A1*, *Glu-B1* and *Glu-D1*) and scored their importance to wheat quality. Later, the combined effects of alleles at both the HMW and low-molecular-weight (LMW) glutenin loci on dough strength were investigated (Eagles et al., 2002; Gupta et al., 1989; Nieto-Taladriz et al., 1994). The HMW and LMW glutenins through disulfide bonds interact to make a gluten network capable of holding the gas evolved during fermentation of the dough (Shewry and Tatham, 1997). A large number of factors have been suggested to affect BMQ such as, lipids (Pomeranz and Chung, 1978), pentosans (D'Appolonia et al., 1970), hydrolytic enzymes and LMW ‘soluble’ proteins within the albumin and globulin fractions (Pogna et al., 1990; Zawistowska et al., 1986). Some of these proteins are enzymes, involved in metabolic processes, while others are amylase and protease inhibitors playing protective roles in plants (Bietz, 1988). Along with quantitative trait loci

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(QTLs) affecting grain protein content (Dholakia et al., 2001; Groos et al., 2003; Prasad et al., 2003; Turner et al., 2004), few studies reported additional genetic loci that influence dough rheology and baking quality (Groos et al., 2004; Law et al., 2005; Perretant et al., 2000).

In order to understand BMQ of wheat many direct and indirect methods are being exploited. The indirect methods include mixograph, farinograph, sedimentation volume and extensograph (Bushuk, 1985). Loaf volume (Lv) is usually considered as one of the most important and direct measures of BMQ (Weegels et al., 1996). However, Lv estimation of bread demands large sample material, cost and labor. Visco-elastic property of wheat proteins is therefore, studied to dissect the genetic effect of loci governing this trait (Ma et al., 2005). Diagnostic markers are available for BMQ influencing parameters like HMW- and LMW-glutenin subunits, PinA, PinB, secalins, grain protein content (Gale, 2005), however, studies on Lv, a main direct estimate of BMQ are limited. Moreover, QTL studies on Lv have suggested that the HMW- and LMW-glutenin subunits cannot be used as indirect measure of Lv (Rousset et al., 2001). Loci on chromosome 3A (Law et al., 2005) and chromosome 2A (Kuchel et al., 2006) were found to control Lv directly. Identifying such loci for Lv would help in implementation of and early progeny selection for BMQ using marker assisted breeding.

The Recombinant Inbred Lines (RILs) population is commonly used to dissect the QTLs associated with quality traits in wheat (Campbell et al., 1999; Kuchel et al., 2006). In order to study Lv, we analyzed a RIL population that was developed from a cross between HI 977 and HD 2329 using SSR markers. The phenotypic traits were analyzed by growing the RIL population in three different agroclimatic conditions in India for 2 consecutive years (2003–2004; 2004–2005). The goals of this study were: (1) to construct framework map using SSR markers (2) to identify Lv QTLs using composite interval mapping (3) to study the Q × E interaction of Lv across different locations and (4) to study the relevance of Glu-1 loci in determining the Lv.

2. Materials and methods

2.1. Plant material

RIL population of F₈ generation comprising 105 lines was derived from a cross between HI 977 and HD 2329. The pedigree for HI 977 was [Gallo/AUST II 61.157 /2/ Ciano 67/NO66 /3/ Yaqui50-Enano/3*Kalyansona] and for HD 2329 was [HD 2252/UP 262]. The cultivar HI 977 has been known for its good BMQ having Glu-A1 (2*), Glu-B1 (17+18) and Glu-D1 (5+10) and HD 2329 for poor BMQ with Glu-A1 (2*), Glu-B1 (7+9) and Glu-D1 (2+12). The population was developed at Directorate of Wheat Research (DWR), Karnal, India by single seed descent from F₂ generation onwards, bulked plantwise at F₈ generation and grown at three different agro-climatic regions (Karnal—North Western plain zone, Kota—

Central zone and Pune—Peninsular zone) for 2 consecutive years, in an augmented block design (Table 3). The RILs were not replicated within a location (Hessler et al., 2002) and the design comprised an Augmented Randomized Complete Block (RCB) design having 8 blocks with 20 lines and 5 replicating checks, in each block. The lines were grown in 2 rows with 2 m × 0.23 m spacing in between the lines. The meteorological data were collected including temperature, humidity and rainfall (Gupta et al., 2002). The data analysis was performed with IRRISTAT (IRRI, Philippines) using “Single site analysis module”. The analysis of variance (ANOVA) revealed significant difference among the genotypes of the population in each location for Lv.

The G × E interaction of RILs with the environments was deciphered by using AMMI (Additive Main effects and Multiplicative Interaction) model with IRRISTAT (IRRI, 2002) software through “Cross site analysis module”. Two year’s data at three sites were treated as six environments in the analysis. The sum of squares was first partitioned into genotype, environment, and G × E interaction, then, the sum of squares for G × E interaction term was further partitioned by principal components analysis using the AMMI model (Crossa et al., 1990; Gauch, 1992) using the formula

$$Y_{ij} = u + g_i + e_j + \sum_{k=1}^n \lambda_k \alpha_{ik} \gamma_{jk} + R_{ij},$$

where Y_{ij} is the value of the i th genotype in the j th environment, u is the grand mean, g_i is the mean of the i th genotype minus grand mean, e_j is the mean of the j th environment minus the grand mean, λ_k is the singular value for the principal component analysis axis k , α_{ik} and γ_{jk} are the principal component scores for principal component analysis axis k of the i th genotype and j th environment, respectively, and R_{ij} is the residual.

Standard error differences between two check means were calculated by $\sqrt{2\text{MSE}/b}$; where ‘MSE’ is error mean sum of square (checks) and ‘ b ’ number of blocks. Broad sense heritability (H^2) using the formula $H^2 = 1 - M_2/M_1$; where M_1 is the mean sum of square due to genotypes and M_2 is the mean sum of square due to genotype × environment (G × E). The adjusted means were calculated for each treatment by interpolation of block effects and used for QTL analysis.

2.2. Lv analysis

The grain samples were tempered (AACC Method 26-10, American Association of Cereal Chemists, 2000) and milled using a Brabender Senior Quadrumat Mill (AACC Method 26-21A) with a ~70% extraction rate. The bread making performance of the flour was determined using the straight dough (AACC Method No. 10-10 B), with the remixing procedure of Irvine and McMullan (1960) with minor modification. The bread formula for each loaf included 100 g flour (14% moisture), 60 ml water, 5 g sugar,

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