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Quantitative trait loci mapping and meta-analysis across three generations for popping characteristics in popcorn

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ABSTRACT

Popping characteristics play a determinant role in the utilization of popcorn (*Zea mays* L.). In this study, the RIL population with 258 recombinant inbred lines was evaluated to detect quantitative trait loci (QTLs) for three popping characteristics (PF, popping fold; PV, popping volume; PR, popping rate) under four environments. Meta-analysis was used to integrate detected QTLs across three generations (RIL, $F_{2:3}$ and BC_2F_2) derived from the same cross. All eleven QTLs were detected for three traits, on chromosomes 1, 2, 4, 6 and 10 for PF, on chromosomes 1, 4, 6, 7 and 10 for PV, and on chromosomes 1, 4, 6 and 10 for PR. Three, 1, 3, 6 and 6 QTL were detected in the same marker intervals in 4, 3, 2, 1 cases, respectively. Four QTLs at bins 1.05–1.06, 1.08–1.09 and 7.03–7.04 were commonly detected in the same or near bins in all three generations. Six and 2 QTLs showed consistency across RIL/$F_{2:3}$ or RIL/BC_2F_2 generations respectively. Nine meta-QTLs (mQTL) were detected on chromosomes 1, 4, 6, 7, 8 and 10. Except mQTL7-1, only related with PV, other mQTLs included two or three traits, reflecting pleiotropic or tightly linkaged QTLs for popping characteristics. The QTL influencing all the three popping traits at bins 1.05–1.06 were also detected in other previous researches using different populations, which could be put into use in marker assisted breeding for popping characteristics in popcorn.

1. Introduction

Popcorn (*Zea mays* L.) is a special kind of corn type being used to make popcorn flake for a series pastime foodstuff. Popping characteristics play a determinant role in the practical utilization of popcorn. According to classical quantitative genetics and traditional statistical analysis, Popping traits were typical quantitative inheritance traits controlled by multiple genes (Ashman, 1983; Clary, 1954). Additive and dominant genetic effects were predominant (Dofing et al., 1991). Moreover, they were influenced by many other factors, such as kernel size, pericarp thickness, endosperm type, amylum type, moisture in the kernel and popping methods, etc., (Allred-Coyle et al., 2000; Mohamed et al., 1993; Singh et al., 1997).

Molecular markers provided a new method to unveil the genetic mechanism in controlling quantitative traits. Mapping QTL for popping characteristics would be of benefit to conduct marker assisted selection (MAS) to overcome the shortcomings of the destructive popping test according to phenotype. Using 3 kinds of temporary genetic segregation populations derived from crosses between popcorn and dent or flint corn inbred lines, QTL for several popping characteristics have been identified on different chromosome regions of the genome, including BC_1 (Lu et al., 2003), BC_2F_2 (Li et al., 2009) and $F_{2:3}$ (Babu et al., 2006; Dhliwayo, 2008; Li et al., 2006, 2007). However, QTL detected for the same trait were highly inconsistent among those researches. Previous reports on other traits also commonly showed that many factors affected the result of QTL mapping, such as material, marker types and densities, population types (Stuber et al., 1992), generations (Austin and Lee, 1996; Li et al., 2009), and environments (Li et al., 2003).

QTL with consistency across populations, generations and environments could be of benefit for efficiency in marker assisted selection (Hospital, 2009). To obtain major QTL with consistency across populations and environments, further extensive studies should be conducted using many distinct populations tested in diverse environments. Moreover, through meta-analysis, QTL detected across several independent studies could be integrated and true QTL with more accurate confidence intervals, genetic

Abbreviations: A, additive; CI, Confidence intervals; CIM, composite interval mapping; CV, variance coefficients; H_B^2, Broad sense heritabilities; LOD, maximum likelihood odds ratio; MAS, marker assisted selection; MIM, multiple interval mapping; mQTL, meta-QTLs; PF, popping fold; PR, popping rate; PV, popping volume; QTL, Quantitative trait loci; RIL, a recombinant inbred lines; SSR, simple sequence repeat.

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correlations among traits and small target regions for candidate genes could be provided (Arcade et al., 2004; Goffinet and Gerber, 2000). Using this method, the consensus-QTL controlling different traits have been revealed in maize (Chardon et al., 2004; Shi et al., 2009).

In our previous researches, QTL for popping characteristics have been detected using $F_{2:3}$ and BC_2F_2 populations derived from the same cross between Dan232 and N04 (Li et al., 2006, 2007, 2009). But for the temporary segregation populations, restricted seed quantity limits the field testing environments. In comparison, RIL populations possess several advantages, such as accessible enough seed to evaluate trait phenotype under multiple environments and improved precise estimate of QTL locations and effects (He et al., 2001). To date, no reports have examined QTL for popping characteristics using RIL population. In this study, QTL for three popping characteristics, popping fold (PF), popping rate (PR) and popping volume (PV), were identified under four environments using RILs population derived from the same cross as $F_{2:3}$ and BC_2F_2 populations in our previous studies (Li et al., 2006, 2007, 2009). Meta-analysis was used to integrate detected QTLs across three generations (RIL, $F_{2:3}$ and BC_2F_2) (Goffinet and Gerber, 2000). Our objectives were: (1) to detect QTL for popping characteristics across three generations and different environments, and (2) to identify consistent and consensus-QTL across generations and environments for further studies in QTL cloning, candidate gene identification and marker-assisted breeding for popping characteristics in popcorn.

2. Materials and methods

2.1. Plant materials and field experiments

The population was developed from a cross between a dent corn inbred Dan232 and a popcorn inbred N04. The Dan232 × N04 cross was made at Changge Agricultural Research Station, Xuchang, Henan Province, China, in 2002. The F_1 was selfed at Sanya winter nursery, Hainan Province, China, in winter 2002. The 258 F_9 recombinant inbred lines (RIL) were developed by single-seed descent from the cross in 2006. Dan232 was derived from Lu 9 kuan × Dan340, which was classified as members of the Ludahonggu heterotic group according to its pedigree. N04 was derived from a Chinese popcorn variety BL03 (Li et al., 2007).

Both parents and 258 F_9 RIL were planted using completely randomized design with one-row plots in four environments in Henan, China, three at Zhengzhou (ZZ1, 34°44′N latitude, 113°42′E longitude), Wenxian (WX, 34°93′N latitude, 113°08′E longitude) and Xinxiang (XX, 35°18′N latitude, 113°54′E longitude) in 2007 with two replications, and one at Zhengzhou in 2008 (ZZ2) with one replication. The rows were 4 m long with 0.67 m spacing between rows. Plots were planted by hand at a density of 60,000 plants per ha. Standard cultivation management practices were used in each environment.

After maturity, ten plants from the middle of each plot were harvested for the evaluation of popping characteristics. The ears were naturally dried until the kernels reached the optimum moisture for popping (13.5 ± 0.5%). The dried ears of each plot were shelled manually and bulked for popping expansion tests. Prior to popping with a BZ-99 popping machine (Shanghai Duoli Food machine building company, Shanghai, China), a sample of 100 kernels from each plot with two replications randomly selected sound kernels were weighed with an electronic balance to measure 100 kernel weight. After popping, the popped volume was measured in the graduated 1 l glass cylinder, while the unpopped kernel volume was measured in a 100 mL graduated measuring cylinder. Popping volume (PV) refers to the popped volume per 100 kernels. Popping fold (PF) was calculated as the total popped volume divided by its 100 kernel weight. Popping rate (PR) was calculated based on the number of popped kernels in 100 kernels after popping. Trait measurements averaged over the two replicate experiments were used as the preliminary data in QTL analyses.

2.2. Phenotypic data analysis

The combined analyses of variance for each trait in 2007 and correlation coefficients among traits for each environment and in the combined analysis were calculated based on a mixed model using the statistical software package SPSS 12.0, with RIL effect random and effects for environments and replications fixed. Broad sense heritabilities (H_B^2) for RIL families on an entry mean basis were calculated as described by Li et al. (2011). H_B^2 and confidence intervals (CI) on heritability estimates were calculated according to Knapp et al. (1985): $H_B^2 = \sigma_g^2/(\sigma_g^2 + \sigma_{gl}^2/n + \sigma_e^2/nr)$, where H_B^2 represents heritability, σ_g^2 is the genetic variance, σ_{gl}^2 is the variance of the interaction of genotype with locations, σ_e^2 is the error variance, r is the number of replications, and n is the number of locations. The estimate values of σ_g^2, σ_{gl}^2, and σ_e^2 were computed from an analysis of variance (ANOVA) using the statistical software package SPSS 12.0 respectively.

2.3. Simple sequence repeat (SSR) and QTL analysis

A total of 207 SSR markers were used to genotype the 258 RILs and construct the linkage map using the same method described by Li et al. (2011). The linkage maps covered 10 maize chromosomes with a total length of 2408.8 cM, and an average interval of 11.6 cM (Li et al., 2011). Composite interval mapping (CIM) (Zeng, 1994) was used to map QTL and estimate their effects for each trait under each environment and in combined analysis as described by Li et al. (2011) using QTL software Windows QTL Cartographer Version 2.5 (Wang et al., 2011). To identify an accurate significance threshold for each trait, an empirical threshold was determined using 1000 permutations (Churchill and Doerge, 1994). QTL positions were ascertained to relevant regions at the point of the maximum likelihood odds ratio (LOD). QTL confidence intervals were calculated by subtracting one LOD value on each side from the maximum LOD position. Based on the results of QTL mapping, interactions among detected QTL were analyzed using multiple interval mapping (MIM) in WinQTLCart (Kao et al., 1999; Wang et al., 2011).

2.4. Integrated QTL map by meta-analysis

Algorithms for meta-analysis were used to estimate the numbers and positions of meta-QTL (mQTL) as described by Li et al. (2011) using BioMercator 2.1 software (Arcade et al., 2004; Goffinet and Gerber, 2000). In our previous studies, two genetic linkage maps were constructed using the $F_{2:3}$ and BC_2F_2 populations derived from the same two inbreds, dent corn inbred D232 and popcorn inbred N04 (Li et al., 2009). A total of 57 QTL for three popping characteristics (PV, PF, PR) were detected in both BC_2F_2 and $F_{2:3}$ populations (Li et al., 2006, 2007, 2009), 33 QTL in $F_{2:3}$ and 22 QTL in BC_2F_2. The integrated genetic map was obtained by projecting the genetic linkage map of $F_{2:3}$ population onto that of the RIL population (Arcade et al., 2004; Goffinet and Gerber, 2000). Meta-QTL analysis was conducted based on data for multiple individual QTL. A modified Akaike's criterion was calculated to select among models with varying numbers of mQTL. For each mQTL, a confidence interval was calculated (Shi et al., 2009).