



Identification of QTLs for storage root yield in sweetpotato



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ABSTRACT

Sweetpotato breeding is challenging due to its genetic complexity, and marker-assisted breeding tools are needed to facilitate the improvement of this crop. In the present study, we identified quantitative trait loci (QTL) for storage root yield of sweetpotato using a mapping population consisting of 202 individuals derived from a cross between Xushu18 (a high yield cultivar) and Xu781 (a low yield line). Two parental linkage maps based on AFLP and SSR markers were constructed using this mapping population. Interval mapping (IM) was performed first and, subsequently, a multiple QTL model (MQM) was used to refine the position and magnitude of the QTL. A total of nine major QTLs for storage root yield were mapped, explaining 17.7–59.3% of the variation. These 9 QTLs, *YIEF.1*, *YIEF.2*, *YIEF.3*, *YIEF.4*, *YIEM.1*, *YIEM.2*, *YIEM.3*, *YIEM.4* and *YIEM.5*, were co-localized to markers E24M1-17d, E53M30-12d, C27.8s**, E63M3-10d, E50M49-4d, IB.S10.9d, E54M5-4d, E21M8-23d and IB.S10.4d, respectively.

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1. Introduction

Sweetpotato, *Ipomoea batatas* (L.) Lam., is the seventh most important food crop in the world. More than 104 million tons are produced globally each year, 95% of which are grown in developing countries (FAOSTAT, 2011). In many developing countries sweetpotato is a staple food crop, which produces large quantities of energy per day comparable to cereals. Simultaneously, it offers the advantages of rich carbohydrates, vitamin A, and tolerance to drought and poor soils (Hagenimana and Low, 2000; Srinivas, 2009). It is also an alternative source of bio-energy as a raw material for fuel production (Ravindran et al., 1995; Santa-Maria et al., 2009; Zang et al., 2009). However, current production is insufficient to meet the rapidly increasing market demand in the world.

Sweetpotato, a highly heterozygous, generally self-incompatible, outcrossing polyploidy with a large number of small chromosomes ($2n=6x=90$), poses numerous challenges for improvement (Shiotani and Kawase (1989); Dhir et al., 1998; Cervantes-Flores et al., 2011). Cross incompatibilities are common and each successful cross typically results in the production of less than two botanical seeds (Cervantes-Flores et al., 2011). Most traits

of economic importance in sweetpotato, including yield, quality, and many resistance traits, are quantitatively inherited or appear to be so due to the polyploid nature of the crop (Cervantes-Flores et al., 2002, 2008). There are often negative correlations among important economic traits of sweetpotato (Ma et al., 1997). Thus, marker-assisted breeding tools are needed for sweetpotato.

Identification of quantitative trait loci (QTL) is an effective approach to examine complex quantitative traits with the application of molecular marker techniques. QTL analysis of major component traits pertaining to storage root yield could be helpful in sweetpotato to locate the favorable alleles and to obtain the recombinants with desirable agricultural traits and, consequently, help breeders in devising strategies for transferring these elite loci from one gene pool to the other excellent gene background. To date, there are only a few reports on the identification of QTL in sweetpotato (Li et al., 2010; Cervantes-Flores et al., 2011; Zhao et al., 2013a,b; Yu et al., 2013). Using a mapping population of the cross Luoxushu 8 × Zhengshu 20, Li et al. (2010) detected one QTL for starch content, explaining only 7.7% of the variation. Cervantes-Flores et al. (2011) identified 13 QTLs for dry-matter content, 12 QTLs for starch content and 8 QTLs for β-carotene content, explaining 15–24% of dry-matter content, 17–30% of starch content and 17–35% of β-carotene content, respectively, using a mapping population derived from a cross between Tanzania and Beauregard. Zhao et al. (2013a,b) and Yu et al. (2013) mapped 27 QTLs for

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dry-matter content and 8 QTLs for starch content, respectively, on the maps of Xushu 18 and Xu 781, explaining 9.0–45.1% and 9.1–38.8% of the variation, respectively.

Mapping of QTL for yield has been performed in hundreds of plants after the development of molecular markers and linkage maps, such as barley (Li et al., 2005), maize (Milena et al., 2006), cotton (Liu et al., 2011), black bean (Wright and Kelly, 2011), bread wheat (Wang et al., 2011; Bennett et al., 2012), rice (Chu et al., 2012), soybean (Kim et al., 2012), cassava (Chen et al., 2012) and juncos (Ramchiary et al., 2007). In sweetpotato, Cevantes-Flores and Jim (2006) and Chang et al. (2009) identified QTLs for storage root yield explaining the variation of 12–30% and 25.1–29.5%, respectively. In a previous study, we developed linkage maps of sweetpotato using amplified fragment length polymorphism (AFLP) and simple sequence repeat (SSR) markers and a mapping population consisting of 202 individuals derived from a cross between Xushu 18 and Xu 781 and mapped QTLs for the storage root dry-matter content (Zhao et al., 2013a,b; Yu et al., 2013). In the present study, we identified QTLs for storage root yield of sweetpotato using this mapping population.

2. Materials and methods

2.1. Mapping population

A mapping population consisting of 202 F_1 individuals derived from a broad cross between two sweetpotato cultivars, Xushu 18 (female) and Xu 781 (male) was used to identify QTLs for the storage root yield. Xushu 18 is the most widely grown sweetpotato in China, and is a high storage root yield and moderate dry-matter cultivar. This cultivar is also resistant to root rot (*Fusarium solani* (Mart.) Sacc. f. sp. *batatas* McClure) and tolerant to sweetpotato feathery mottle virus (SPFMV), but susceptible to stem nematodes (*Ditylenchus destructor* Thorne). Xu 781 is a line selected from bulked seeds of JPKY0-015 in an open-pollinated poly-cross, and has low storage root yield and high dry-matter. It is susceptible to root rot and SPFMV, but resistant to stem nematodes (Li et al., 2003a,b). The population development and AFLP/SSR map construction were described in detail by Zhao et al. (2013a,b).

2.2. Field design and storage root yield determination

The 202 F_1 progeny and both parents were planted at two different locations each year during 2010–2012, Langfang Experimental Station, Langfang, Hebei, China (39°53'94"N, 116°67'46"E) and National Sweetpotato Improvement Center, Xuzhou, Jiangsu, China (34°27'50"N, 117°30'31"E). The field trial was arranged in a randomized complete block design (RCBD) with three replications per experiment. Each plot contained 20 plants spaced at 25 cm within rows and 80 cm between rows. All of the experiments were conducted under normal field conditions. Approximately 100 days after planting, the experiments were harvested and storage root yield in kilograms was directly determined for five plants randomly sampled from the middle 16 plants except for 2 plants per end.

2.3. QTL mapping

The development of the Xushu 18 × Xu 781 genetic linkage map was described by Zhao et al. (2013a,b). The linkage map for Xushu 18 included 90 linkage groups with 2077 markers (1936 AFLP and 141 SSR), and the map for Xu 781 contained 90 linkage groups with 1954 markers (1824 AFLP and 130 SSR). The 13 and 14 homologous groups were identified in Xushu 18 and Xu 781 maps, respectively.

Prior to the QTL analysis, analysis of variance (ANOVA) procedures (SAS 9.1 SAS Institute, Cary, NC, USA) were used to determine if there were any significant differences between the replications

of our experiments within each location and by year. The storage root yield in each environment and the mean data was used for the subsequent QTL detection in the light of the linkage maps.

MapQTL software 4.0 has been used for QTL analysis in several polyploidy plants such as yam (Mignouna et al., 2002), ryegrass (Faville et al., 2003) and sweetpotato (Zhao et al., 2013a,b). In the present study, MapQTL software 4.0 was used to analyze QTLs for storage root yield of sweetpotato. The population was analyzed as an F_2 population in the configuration. Interval mapping (IM) was performed first and, subsequently, a multiple QTL model (MQM) was used to refine the position and magnitude of QTL with MapQTL software 4.0 (Van Ooijen, 2004). An initial set of co-factors was constituted with markers identified as significant from IM analysis. Each linkage group was then screened individually for additional significant ($P < 0.02$) co-factors by extending the initial co-factors set with markers from that linkage group at 5 cM intervals, followed by automatic co-factor selection. Significant co-factors were fixed before proceeding to the next linkage group. Finally, the co-factor was re-adjusted to incorporate the marker with the highest LOD value at each MQM QTL. A single LOD of 2.5 was used as the threshold to determine the presence of different QTL. QTL detected at the same genomic location in at least two different environments and the mean data was considered a single QTL. The final linkage maps with QTLs for storage root yield were drawn using MapChart 2.2 (Voorrips, 2002).

3. Results

3.1. Phenotypic evaluation

The storage root yield of the mapping population was abnormally distributed based on each environment and the mean data (Fig. 1), similar to the results of Brondani et al. (2002) in rice, in which the distribution frequency of yield-related traits fitted abnormal distributions. He et al. (2005) detected QTLs for seed cotton yield which showed abnormal distribution in tetraploid cotton. An et al. (2010) mapped QTLs for 100 seed weight with abnormal distribution in upland cotton. The average storage root yield of the mapping population in all six environments ranged from 0.31 kg to 1.38 kg with a population mean of 0.82 kg. The average storage root yield of Xushu 18 and Xu 781 was 2.04 kg and 0.83 kg, respectively. ANOVA of the storage root yield showed that there were significant effects for year, location and interactions between location and year (Table 1). Therefore, data from each environment and the mean were used for the QTL analyses. Transgressive segregation was also observed in the mapping population, with some individuals exhibiting higher levels and others lower levels of storage root yield than either parent (Fig. 1).

3.2. QTL mapping

A total of 45 QTLs for the storage root yield were detected in each environment and the mean data, explaining 10.2–59.3% of the variation, and nine of them were identified at the same genomic location in at least two different environments and the mean data, explaining 36.3–59.3% of the variation (Table 2).

Four QTLs for the storage root yield, named *YIEF.1*, *YIEF.2*, *YIEF.3* and *YIEF.4*, were identified on four linkage groups of Xushu 18, XUSHU18(01.01), XUSHU18(03.16), XUSHU18(11.55) and XUSHU18(13.62), respectively, and explained 36.3–59.3% of the variation in storage root yield (Table 2, Fig. 2). Three, *YIEF.2*, *YIEF.3* and *YIEF.4*, of the 4 QTLs had a positive effect on storage root yield and explained 59.3%, 42.9% and 44.0% of the variation, respectively (Table 2). In particular, the QTL *YIEF.2* accounted for 59.3% of the variation, and is the QTL which explains the highest

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