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RESEARCH ARTICLE

Genetic dissection of the developmental behavior of plant height in rice under different water supply conditions



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Abstract

Plant height (PH) is one of the most important agronomic traits of rice, as it directly affects the lodging resistance and the high yield potential. Meanwhile, PH is often constrained by water supply over the entire growth period. In this study, a recombinant inbred line (RIL) derived from Xiaobaijingzi and Kongyu 131 strains grown under drought stress and with normal irrigation over 2 yr (2013 and 2014), respectively (regarded as four environments), was used to dissect the genetic basis of PH by developmental dynamics QTL analysis combined with QTL×environment interactions. QTLs with net effects excluding the accumulated effects were detected to explore the relationship between gene×gene interactions and gene×environment interactions in specific growth period. A total of 26 additive QTLs (A-QTLs) and 37 epistatic QTLs (E-QTLs) associated with PH were detected by unconditional and conditional mapping over seven growth periods. *qPH-2-3*, *qPH-4-3*, *qPH-6-1*, *qPH-7-1*, and *qPH-12-5* could be detected by both unconditional and conditional analyses. *qPH-4-3* and *qPH-7-5* were detected in four stages (periods) to be sequentially expressed QTLs controlling PH continuous variation. QTLs with additive effects (A-QTLs) were mostly expressed in the period S3|S2 (the time interval from stages 2 to 3), and QTL×environment interactions performed actively in the first three stages (periods) which could be an important developmental period for rice to undergo external morphogenesis during drought stress. Several QTLs showed high adaptability for drought stress and many QTLs were closely related to the environments such as *qPH-3-5*, *qPH-2-2* and *qPH-6-1*. 72.5% of the QTLs with *a* and *aa* effects detected by conditional analysis were under drought stress, and the PVE of QTLs detected by conditional analysis under drought stress were also much higher than that under normal irrigation. We infer that environments would influence the detection results and sequential expression of genes was highly influenced by environments as well. Many QTLs (*qPH-1-2*, *qPH-3-5*, *qPH-4-1*, *qPH-2-3*) coincident with previously identified drought resistance genes. The result of this study is helpful to elucidating the genetic mechanism and regulatory network underlying the development of PH in rice and providing references to marker assisted selection.

Keywords: rice, plant height, drought stress, QTL, developmental behavior, environment interactions

Received 7 December, 2015 Accepted 31 May, 2016
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doi: 10.1016/S2095-3119(16)61427-2

1. Introduction

Rice (*Oryza sativa* L.) is one of the most important grain crops globally, and more than half of the world's population lives on it. Plant height (PH) is an important agronomic trait in rice, as it determines plant architecture and greatly influences the grain yield (Machado *et al.* 2002; Venuprasad

et al. 2009). Excessive PH will help improve the ventilation conditions of the group and accommodate more leaves, but it will cause lodging (Setter et al. 1997). Overly short plant height will cause crowded leaves, poor ventilation and diminished light conditions, leading to reduced photosynthetic efficiency (Peng et al. 1994).

PH in rice is generally considered to be controlled by both qualitative and quantitative genes (Huang et al. 1996). According to incomplete statistics, over 1 000 QTLs related to rice PH have been detected (www.gramene.org/db/qlt) that are distributed on 12 chromosomes, but relatively few QTLs have been cloned. Valuable QTLs that could be used in rice breeding are rare. *sd-1*, the “Green Revolution” gene encoding gibberellic acid 20 (GA₂₀) oxidase has been cloned by Monna (2002), Spielmeier (2002) and Madoka (2002) and catalyzes the conversion of GA₅₃ to GA₂₀. Xue et al. (2008) cloned an important QTL, *Ghd7*, which controlled PH, the number of grains per panicle and the heading date. It encodes a CCT (CO, CO-LIKE and TIMING OF CAB1) structural protein consisting of 257 amino acids with a CCT structural domain that has many similarities and obvious difference with the nuclear protein CONSTANS (CO) of *Arabidopsis*.

The growth of rice PH is a dynamic process reliant on complex genetic mechanisms. Most of the previous studies on QTLs related to PH focused on unconditional QTL analysis, which can only dissect the cumulative effect of PH gene expression (Zhang et al. 2008; Lee et al. 2014; Saikumar et al. 2014). Conditional QTL analysis (Zhu 1995) based on developmental dynamics can better explain the sequential expression of genes. The method has revealed new genetic variations arising at specific periods during ontogeny. The conditional QTL accounts for gene expression at a specific developmental period ($t-1 \rightarrow t$), and explains the variation of traits from a dynamic sequential perspective. Time-related QTL mapping has been used to reveal the genetic basis of developmental characteristics of rice PH (Yan et al. 1998a; Cao et al. 2001; Septiningsih et al. 2003; Yang et al. 2006). The combination of conditional and unconditional analyses is a more effective way to dissect the QTL expression of rice PH, as it interprets important growth periods of PH from a primary QTL explanation standpoint and reveals the genetic bases for PH development.

PH is a trait modified by the environment. A limited water supply often inhibits PH development, consequently affecting yield (Zhuang et al. 1997; Babu et al. 2003; Lanceras et al. 2004; Vikram et al. 2011). As an important component of yield, PH regularly appears in QTL mapping studies under drought stress. As it provides an effective unbiased analysis of quantitative traits, QEI (QTL×environment interaction) is an important component of quantitative traits inheritance in addition to the additive and epistatic effects.

The QEI phenomenon is ubiquitous between genes and the environment. Changes in environmental conditions can easily lead to changes in gene expression because of the continuous variation of quantitative traits (Cao et al. 2001; Kato et al. 2008; Wu et al. 2010). Some studies were performed on the QTL×environment interaction of PH (Li et al. 2003; Lanceras et al. 2004; Zhang et al. 2008), but all of them focused on unconditional QTL analysis. So far, few reports have documented the dynamic QTL analysis for rice PH combined with QEI. The objective of this research was to map the loci of the primary genetic effects and QE effects underlying the developmental behavior of rice PH by unconditional and conditional genetic models. The genetic basis of PH development was studied under normal irrigation and drought stress, both individually and combinedly. We tried to investigate the developmental genetic behavior of rice PH in different environments and explore the net genetic effects of QTLs in specific growth period. Providing references for plant type improvement and drought resistance breeding in rice.

2. Materials and methods

2.1. Experimental materials

207 F_{6,7} and F_{6,8} recombinant inbred lines (RILs) derived from Xiaobaijingzi (XJ)×Kongyu 131 (K131) were respectively used in the present study in 2 yr (2013 and 2014). The two parents differed greatly in morphological and physiological characteristics. XJ is an upland *japonica* approximately 115 cm tall with a spike length of 17.6 cm and weak tillering ability, imported from the Chinese Academy of Agricultural Sciences. The whole growth period of XJ is 128 d. K131 is a *japonica* approximately 80 cm tall with a spike length of 14.0 cm and strong tillering ability, cultivated widely in northeast of China but its drought resistance is weak. The whole growth period of K131 is 125 d. The two parents differed a lot in drought resistance and plant height (Xing et al. 2014). Transgressive segregation of heading date occurred between the RILs (Appendixes A and B), but it did not greatly affect the measurement of PH.

2.2. Field experiments

The 207 RILs and the two parents were planted at the experimental station of Northeast Agricultural University, Harbin (126°7'E, 45°8'N), China, in 2013 and 2014 with three replicates in a completely randomized design. The treatment was drought stress with normal irrigation as the control. Under normal irrigation, water remains 2–10 cm above the soil surface. Since the water distribution of northeast of China is uneven, we set drought-stressed treatments as

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