

QTLs for Spikelet, Panicle and Grain Numbers in Rice (*Oryza sativa*L) : A Review

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ABSTRACT

Rice spikelets are borne on the branches of an inflorescence known as a panicle. The weight of an individual rice grain for a cultivar is almost constant. Consequently, yield improvements in a rice cultivar are always associated with an increase in grain number per unit ground area. Understanding the relationship between the number of spikelets when they differentiate and the number of grains at harvest is important in understanding the basis of high yield in rice. Effective panicle number, grain number, and grain weight are the three components of rice yield, of which grain number shows the highest variation and makes the largest contribution to yield output. Rice panicle number per plant is a grain yield component that directly influences rice yield. The identification of the genes controlling panicle number will play a vital role in high -yield rice breeding. Studies on QTL of panicle number in rice are limited to morphological description and primary mapping. Rice grain number is quantitatively inherited and great deals of quantitative trait locus (QTL) mapping for grain number have been conducted using various mapping populations. Panicle morphology and grain number are influenced by the development of the panicle main axis, primary and secondary branches, spikelet development, and developmental phase transitions. Grain number is linearly correlated with total plant N content.

Keywords: QTL, Panicle, Grain number, spikelet, *Oryza sativa*

I. INTRODUCTION

With the advent of DNA molecular markers, QTL mapping has become a routine strategy for the discovery of genes involved in complex quantitative traits. Thousands of QTL have been mapped for important agronomical traits in rice. Although primary mapping populations including F₂, recombinant inbred lines (RILs) and doubled haploid lines (DHs) have been widely used for QTL mapping in rice (Li et al., 1995; Yu et al., 1997; Xu et al., 2004; Fan et al., 2005; Marri et al., 2005), QTL can only be localized to a genomic region (confidential region) rather than a locus in those populations. Following the primary mapping, advanced populations such as near isogenic lines (NIL) and chromosome segment substitution lines (CSSL) can be used to map QTL to a locus as a Mendelian factor by blocking the genetic background noise (Lin et al., 2002;

Zhang et al., 2006; Wang et al., 2006). Based on this strategy, several QTLs have been isolated in tomato (Frery et al., 2000) and rice (Yano et al., 2000; Takahashi et al., 2001; Li et al., 2003) in recent years. The common aspect in all the QTL cloning work is to exploit high quality NILs as advanced mapping populations. Rice is a staple food for many countries. As the world population increases, rice production has to be raised by at least 70% over the next three decades to meet growing demands. In the long run, development of high yield varieties is one of the most important goals in rice cultivation. Complex traits such as rice yield components are quantitative inheritance, which are contributed by multiple genes each with small effect, namely quantitative trait loci (QTL). Number of spikelets per panicle (SPP) is highly associated with number of grains per panicle (GPP), which is a very important component of yield. These traits have been

frequently studied because of their importance in rice genetic improvement with the advent of the molecular markers (Xiao et al., 1996; Zhuang et al., 1997; Xiong et al., 1999; Xing et al., 2002, 2008). Rice spikelets are borne on the branches of an inflorescence known as panicle. The number of spikelets per panicle (SPP) is strongly influenced by primary and secondary branches and is also important for determining yield potential in rice (Zhang et al., 2006). Many studies have detected quantitative trait loci (QTLs) for SPP using various segregating populations (Thomson et al., 2003; Suh et al., 2005; Liu et al., 2010). These QTLs are located across the chromosomes and provide valuable information on the genes that control SPP in different populations.

A. Nitrogen fertilizer increases spikelet number per panicle

Growing populations will demand higher rice yield, which is partly limited by flower number per panicle. Therefore, increasing the flower number per panicle via breeding and/or crop management is indispensable for increasing rice yield. Nitrogen fertilizer might affect cytoKinin (CKs) levels to increase rice flower numbers. A correlation between nitrogen nutrition and CKs was demonstrated many years ago (Hirose et al., 2008; Salama & Wareing, 1979). CKs regulate rice branch and flower numbers (Barazesh & McSteen, 2008). CKs oxidase/dehydrogenase (OsCKX) is an enzyme that degrades CKs and, in many plant species, is responsible for the majority of metabolic CKs inactivation (Werner et al., 2003). Reduced expression of OsCKX2 causes CKs accumulation in inflorescence meristems and increases the number of reproductive organs and yield (Ashikari et al., 2005).

B. A model explaining genotypic and environmental variation of rice spikelet number

Many hypotheses have been proposed to explain ecophysiological processes that determine spikelet number per unit area. Those hypotheses may be classified into the following three types. The first is that the spikelet number is proportional to nitrogen (N) content of plant (product of percentage N and crop biomass per unit area) at around spikelet formation stage (Murayama, 1969; Hasegawa et al., 1994; Kobayashi & Horie, 1994; Horie et al., 1997). The second is that the

spikelet number is proportional to biomass production during the period from panicle initiation to heading (Kropff et al., 1994). The third is that the final spikelet number is represented as the difference between the numbers of spikelets differentiated and degenerated; the former is proportional to the crop-N content at the late spikelet differentiation stage and the latter to crop growth rate (CGR) during the period from the late stage of spikelet differentiation to heading (Wada, 1969).

C. Characterization of near-isogenic lines carrying QTL for high spikelet

Grain yield of rice (*Oryza sativa* L.) has four components: panicle number, total spikelet number per panicle (TSN), grain weight and spikelet fertility. There is wide variation in TSN among cultivated rice varieties and it is one of the targets of breeding programs to improve rice yield. However, genetic analysis of TSN is difficult because it is a complex trait controlled by multiple genes and influenced by environmental conditions. Quantitative trait locus (QTL) analysis using DNA markers has recently made it possible to understand the genetic basis of TSN and other complex traits. QTLs for TSN have been identified using various segregating populations, including F₂ populations, recombinant inbred lines (RILs), and doubled haploid (DH) lines (Hittalmani et al., 2003; Kobayashi et al., 2004; Mei et al., 2005; Xing et al., 2002; Yagi et al., 2001; Zhuang et al., 1997; Zou et al., 2005). Since the 1960s, IRRI-bred rice varieties have been distributed worldwide and used by both plant breeders and farmers. IR64, which was released in 1985, had been widely accepted as a high-quality rice variety in many countries (Khush, 1987). Because of the wide adaptability of IR64, breeding materials with an IR64 genetic background, such as DH lines, RILs and thousands of mutant lines, have been developed for research and improvement of rice varieties (Guiderdoni et al., 1992; Wu et al., 2005). In the late 1980s, a breeding program to develop a new plant type (NPT) of rice was launched at IRRI with the goal of increasing yield potential under tropical environments. Unlike IR64, the NPT varieties have several agronomic traits inherited from tropical *japonica*-type varieties: low tiller number, low number of unproductive tillers, large panicle, thick culm, lodging resistance and large, dark green flag leaves (Khush, 1995). Thus, the NPT varieties were

chosen for experiments designed to improve the yield potential of IR64.

D. A novel gene controlling the number of grains per panicle in rice

Rice yield is a complex trait multiplicatively determined by three component traits: number of panicles, grain weight and number of grains per panicle (NGP) (Hua et al., 2002). Of these, NGP is shown to be highly correlated with yield and acts as a crucial component in determining rice yield (Luo et al., 2013). Therefore, dissection of its genetic basis would be of great value in breeding high-yielding rice varieties. During the last decade, although many QTLs/genes controlling the NGP trait have been mapped in rice (Tian et al., 2006; Ahmadi et al., 2008; Xing et al., 2008; Liu et al., 2009; Deshmukh et al., 2010; Zhang et al., 2013), only a few related genes have been cloned (Ashikari et al., 2005; Huang et al., 2009; Tabuchi et al., 2011), and the molecular mechanism of NGP trait formation is still far from clear. Genetic analysis indicates that the *ngp4c* phenotype is controlled by a single recessive gene, tentatively named as *NGP4c(t)* and the *NGP4c(t)* gene was finally mapped to 81.7 kb region, where no gene involved in the NGP trait formation had been reported previously.

E. Genetic mapping of a QTL controlling leaf width and grain number in rice

Panicle morphology and grain number are influenced by the development of the panicle main axis, primary and secondary branches, spikelet development, and developmental phase transitions. The transition from the adult phase to the reproductive phase involves the participation of sucrose, miR156, and miR172 (Tsai & Gazzarrini, 2014; Zhu & Chris, 2011). During this transition, the gain-of-function mutation of *OsSPL14* causes release from suppression by miR156, and the grain number is increased owing to the accelerative development of secondary branches (Jiao et al., 2010; Miura et al., 2010). Two major quantitative trait loci (QTLs), *qGNPP1-1* and *qFLW1-1*, which control grain number per panicle and flag leaf width, respectively, were detected by QTL analysis on the same interval of chromosome 1 between markers RM3521 and RM8111 using an F₂ population derived from the cross HP× Nipponbare. Thus, a single QTL, designated *qLG1* (Leaf

width and grain number 1), was presumed to control both traits (Tian et al., 2014).

F. Designing and Validation of Primers for High grain number

The cultivated rice (*Oryza sativa* L.) is rich in genetic diversity apart from highly diverse 21 wild progenitors and the African cultivated rice, *Oryza glaberrima* Steud. In addition to staple food, rice has extensive protective and curative properties against human ailments like epilepsy, chronic headache, rheumatism, paralysis skin diseases, diabetes, arthritis, indigestion, blood pressure, colon cancer, internal rejuvenation of tissues and overcoming postnatal weaknesses. Three hundred sixty nine QTLs distributed across all over the 12 chromosomes of rice controlling grain number per panicle have been identified (<http://www.gramene.org>) using various mapping populations derived from inter-specific indica-japonica, indica-indica and japonica-japonica crosses. Some of them were fine mapped to less than 1 cM intervals and few have been cloned using QTL-based near isogenic lines (NIL). Genes controlling grain number per-panicle directly or indirectly, i.e. *Gn1a*, *Ghd7*, *Dep1*, *fz*, *Sp1*, *rcn2*, *lax1* and *Apo1* also have been isolated from rice (Jin, 2008; Li, 2009; Piao, 2009; Zha, 2009).

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