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Genes offering the potential for designing yield-related traits in rice

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Breeding of high-yielding rice is crucial for meeting the food demand of the increasing world population. New technologies have facilitated identification of genes involved in quantitative traits, and many genes underpinning quantitative trait loci involved in rice crop yield have been isolated. Meanwhile, various kinds of mutants have been intensively studied, leading to characterization of many genes related to yield traits. A combination of quantitative trait locus analysis and studies of such mutants has made it possible to compile a list of genes available for breeding rice with higher yield.

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Introduction

Along with maize and wheat, rice is one of the world's three major cereal crops, and it is produced mainly in Asian countries. Increasing yield has been set as the overriding objective of breeding for many years for all these crops, and is absolutely essential for overcoming an impending food crisis caused by the increase in the world's population. Rice yield is determined by several factors including number of plants per unit area, number of tillers per plant, number of grains per panicle, and grain size. Understanding the mechanisms that govern these yield traits is critical in order to optimize the combination of the component traits for high yield.

Traits can be divided into two classes, qualitative and quantitative; the former are controlled by one or a few loci and the phenotypes segregate into discrete classes according to Mendelian inheritance, whereas the latter are controlled by multiple genes called quantitative trait loci (QTLs) and show continuous phenotypic variation. Many agronomically important traits including crop yield are governed by QTLs. Completion of the whole genome sequence of rice and subsequent innovations in genotyping technology have greatly accelerated QTL analysis, and many QTL genes relevant to crop yield have been isolated.

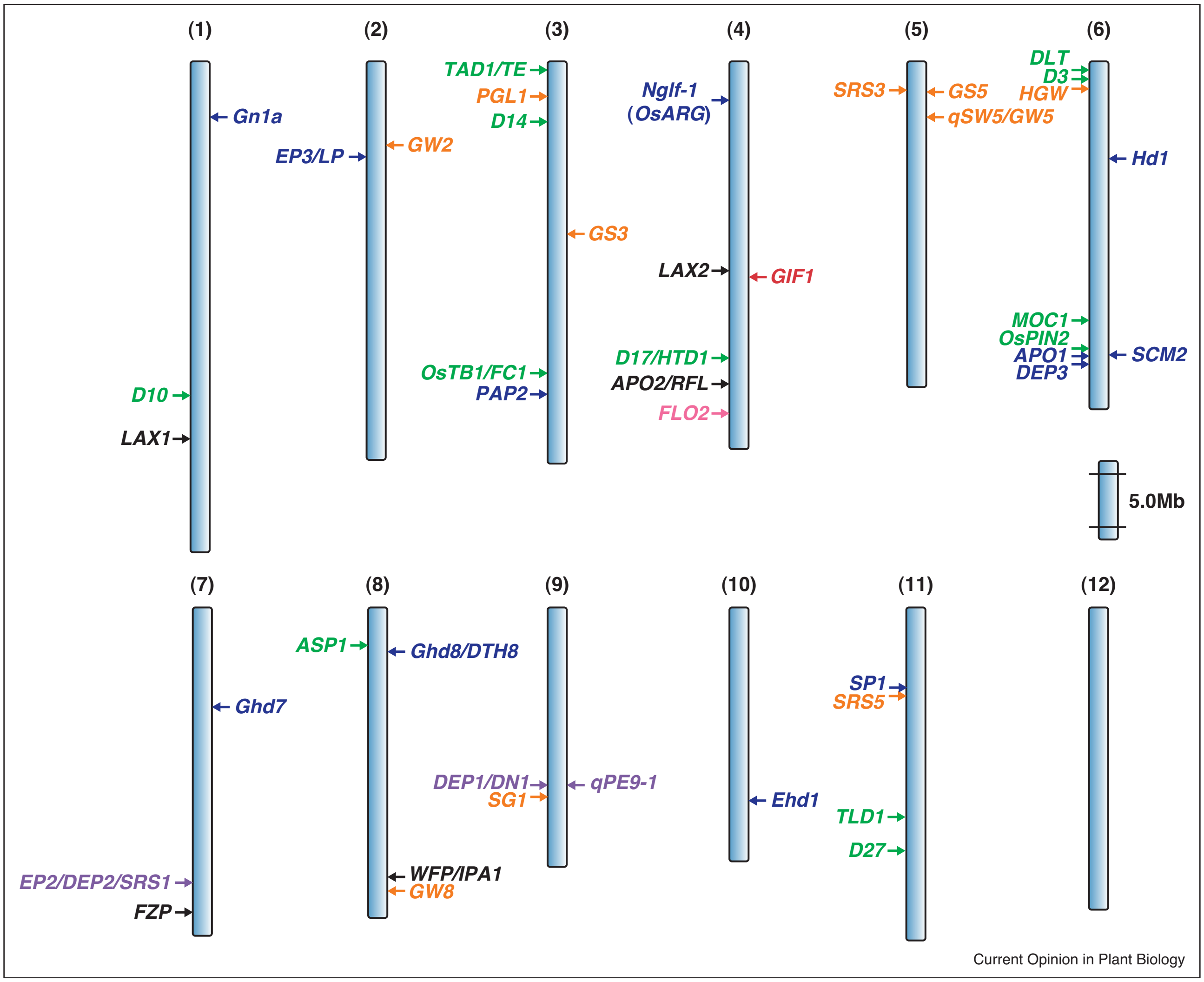
In the past, on the other hand, many mutant lines of rice have been generated and characterized [1]. Although mutants are very useful for elucidating regulatory mechanisms, especially for developmental processes including those of panicles and flowers, their value in rice breeding is limited because they almost always cause an inferior phenotype in terms of crop production. Recently, however, there have been a few reports that QTL genes involved in some agronomically important traits are identical to causal genes of mutants (Figure 1 and Table 1). This leads us to speculate that genes identified for mutants might also be useful targets for molecular breeding of rice. Thus, in this review, we focus on both QTLs and mutants related to factors affecting crop yield such as panicle branching pattern, grain number, panicle number, and grain size and filling. As there have been several good reviews describing similar topics especially in QTL studies [2–4], we only briefly comment on genes mentioned in previous reviews, focusing mainly on new reports here.

Panicle branching pattern and grain number

The branching habit of a panicle is a trait that determines grain yield. The rice panicle is an assembly of multiple orders of branches, described as primary, secondary, and tertiary rachis branches, and seed grains are attached at the end of each complexly branching rachis. Therefore, it is important to elucidate how development of the rachis is genetically controlled and how the branching structure is determined.

Using QTL analysis of population derived from a cross between varieties Koshihikari and Habataki, Ashikari *et al.* [5] isolated *Grain number 1a* (*Gn1a*) as the most effective QTL gene, which increases the grain number, mainly by increasing the secondary rachis branching. This was the first report on isolation of a QTL gene from rice. Later, *STRONG CULM 2* (*SCM2*), which is identical to *ABERRANT PANICLE ORGANIZATION 1* (*APO1*), previously isolated as the causal gene of a mutant with

Figure 1



Map position of the cloned QTLs/genes involved in yield traits of rice. Arrows at the left or right indicate the position of each gene identified in a mutant or QTL, respectively. The color of arrows indicates each trait; blue for 'panicle branching pattern (PBP) and grain number (GN)', black for 'PBP and GN and panicle number', purple for 'PBP and GN and grain size', green for 'panicle number', orange for 'grain size', pink for 'grain size and filling', and red for 'grain filling.'

aberrant panicle structure, was also identified using the same population as a QTL controlling both the rachis branch number and culm size [3,4,6•].

WEALTHY FARMER'S PANICLE (*WFP*) and *Ideal Plant Architecture 1* (*IPA1*) were independently isolated and identified as the same QTL gene regulating the number of primary rachis branches per panicle and leading to an increase in grain number [7,8]. This gene encodes SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 14 (OsSPL14), an SBP-box protein targeted by miRNA156.

Two other QTLs related to grain number, *Grain number, plant height and heading date 7* (*Ghd7*) and *Ghd8*/*Days to heading 8* (*DTH8*) have also been identified [3,4,9•]. These QTLs pleiotropically regulate grain yield, heading date, and plant height. Both act upstream of *Early heading date 1* (*Ehd1*) and *Heading date 3a* (*Hd3a*) in the photoperiod-controlled flowering pathway. Recently, Endo-Higashi and Izawa [10] suggested that *Heading date 1* (*Hd1*) and *Ehd1* jointly control the number of primary rachis branches, and that their control of panicle size via flowering time genes may be mediated by the expression of *Hd3a* and *RICE FLOWERING LOCUS T 1* (*RFT1*) in rice leaves at the time of floral transition.

DENSE AND ERECT PANICLE 1 (*DEP1*)/*DENSE PANICLE 1* (*DN1*) was identified as the causal gene of