REVIEW

Genetic and Molecular Insights into the Enhancement of Rice Yield Potential

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Abstract Rice is one of the most important global food crops and a primary source of calories for more than half of the world's population. Rice production increased steadily during the green revolution era primarily as a result of introducing high-yielding rice varieties. World rice production increased at a rate of 2.3–2.5% per year during 1970s and 1980s, but this rate of growth was only 1.5% per year during the 1990s. The yield growth rate for rice has further declined during the first decade of this century. However, the populations in the major rice-consuming countries continue to grow at a rate of more than 1.5% per year. According to various estimates, world rice production must increase at the rate of 2 million tons per year. To meet this challenge, rice varieties with higher yield potential and greater yield stability are needed. Various strategies for increasing the yield potential of rice include; (1) conventional hybridization and selection, (2) F_1 hybrid breeding, (3) modification of plant architecture, and (4) enhancement of photosynthesis. Many genes and QTLs have recently been identified which will assist with rice breeding objectives.

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Introduction

Rice (*Oryza sativa* L.) is the most important food source for more than half of the world's population. Major advances in increasing rice production have occurred during the last four decades through the adoption of green revolution technologies based primarily on the availability of high yield varieties. World rice production increased at the rate of 2.3–2.5% per year during 1970s and 1980s. However, during the 1990s, this growth rate has reduced to 1.5% annually. This yield growth rate has further declined during the present decade (http://www.fao.org/docrep/005/ac484e/ac484e08.htm). For example, the average rice yield in China increased from 5.4 to 6.4 t/ha between 1987 and 1997, but no clear increase was achieved between 1997 and 2007 (Peng et al. 2009). Significantly, the number of rice consumers is growing at the rate of 1.5% per year, whereas rice production is now only increasing at the rate of 1.0% per year. To make up this shortfall, rice stocks are being accessed, but global rice stocks have declined from 147 million tons in 2001 to 82 million tons in 2008 (Mohanty et al. 2010).

According to UN estimates, the world's population will increase from 6.7 billion at present to 8 billion in 2025 (http://www.un.org/esa/population/publications/longrange2/WorldPop2300final.pdf). According to various estimates,

world rice production must increase from 440 million tons at present to 475 million tons in 2020 (Mohanty et al. 2010). The FAO estimates that world rice requirements will be 524 million tons in 2050, requiring a yearly increase of 2 million tons from the present production levels. If this challenge of producing more rice from existing land resources is to be met, rice varieties with a higher yield potential will be required. In this review, we summarize the various genetic and molecular approaches that are currently being adopted to increase the yield potential of rice. These include (a) conventional hybridization and selection; (b) F_1 hybrid breeding; (c) modification of the plant architecture; and (d) enhancement of photosynthesis.

Conventional Hybridization and Selection

Traditional cross hybridization and selection is still a widely used strategy for developing cultivars with a higher yield potential. In this methodology, the segregating populations derived from crosses between two parents are screened for desirable recombinants, and selected fixed lines are evaluated in replicate yield trials. This approach is therefore based on the variability created through hybridization between diverse parents and the subsequent selection of desirable individuals. Cross hybridization and selection has contributed on average to about a 1% increase per year in the yield potential of rice since the development of IR8, the first improved semidwarf (short statured) rice variety (Peng et al. 2000). However, hybrid sterility in rice can often hinder the transfer of useful genes during intersubspecific crosses. The molecular basis of this hybrid sterility is usually complex, often involving the cumulative effects of gene interactions at multiple loci (Ouyang et al. 2010).

In recent studies, two hybrid sterility genes, S5 and Sa, involved in the indica–japonica subspecies hybrid sterility, have been cloned (Chen et al. 2008; Long et al. 2008). The hybrid female sterility gene S5 was found to encode an aspartic protease. Interestingly, among the three indica (S5-i), japonica (S5-j), and neutral S5 (S5-n) alleles in rice, S5-n carrying variety produced fully fertile hybrids from a heterozygous genetic background with either of the incompatible alleles (Chen et al. 2008). The Sa locus, involved in conditioning hybrid sterility, was found to consist of two adjacent genes, SaM encoding a small ubiquitin-like modifier E3 ligase-like protein, and SaF encoding an F-box domain-containing protein (Long et al. 2008). This study also identified three Sa haplotypes (indica, japonica, and compatible), thus proposing a two gene/three component interaction model for hybrid sterility. Hence, the introgression of these wide-compatibility genes (WCGs; neutral or compatible alleles) may provide

a means to break the sterility barrier between indica and japonica subspecies.

Crop gene pools have been increased through the hybridization of cultivated rice with wild rice species (Brar and Khush 1997). These pools have made it possible to improve a number of important traits including yield potential. As an example, some backcross derivatives from a cross between Oryza rufipogon from Malaysia and cultivated rice resulted in a strain with an 18% greater yield than the recurrent parent. The increased yield potential of these interspecific derivatives has been attributed to higher vegetative growth rates or early seedling vigor (Xiao et al. 1996). Hybrid incompatibility in the F_1 generation between specific cultivars and their wild relatives is often a major reproductive isolation barrier. Recently, the reciprocal loss of duplicate genes encoding mitochondrial ribosomal protein L27 at two loci, S27 and S28, was found to cause pollen sterility in hybrids of O. sativa and its wild relative Oryza glumaepatula (Yamagata et al. 2010). Furthermore, this demonstrated that the introduction of a functional allele, essential for the later stage of pollen development, could overcome hybrid sterility between cultivated rice and wild relatives.

F_1 Hybrid Breeding

Hybrid breeding exploits the increased vigor or heterosis of F_1 hybrid plants that is usually observed in crossbred species. In maize, a major yield improvement has been associated with the introduction of commercial hybrids. The average yield advantage of hybrids versus cultivars is approximately 15% (Tollenaar 1994). In rice, hybrids between indica×indica and indica×japonica lines have been investigated.

Three main strategies for hybrid rice breeding have been proposed: the three-line method using the cytoplasmic male sterility (CMS) system; a two-line method using the photoperiod-sensitive genic male sterile (PGMS) and thermo-sensitive genic male sterile (TGMS) system; and a one-line method using the apomixis system (Virmani and Kumar 2009). Existing rice hybrid varieties that are used commercially are mainly intervarietal hybrids that are based on the three-line method. This CMS F_1 hybrid breeding system requires two lines carrying either a sterile (S) or normal (N) cytoplasm and a third line harboring nuclear fertility restorer (Rf) genes. To generate fertile F_1 hybrids, a cytoplasmic male sterile line is mated with the Rf restorer line. The resulting hybrid seeds are fertile. The cytoplasmic male sterile line is also maintained by crossing it with a normal cytoplasm line (Khush 2001; http://www.fao.org/docrep/006/Y4751E/y4751e0f.htm). Rice hybrids with a yield advantage of about 10–15% over the best known

inbred varieties were introduced in China in mid-1970s and now account for about 50% of the rice grown (IRRI 2004). Rice hybrids that are adapted to tropical climates have been bred at the International Rice Research Institute (IRRI) and by several National Rice Improvement programs.

Modification of Plant Architecture (Ideotype Breeding)

Ideotype breeding is designed to modify the plant architecture and is a proven strategy to improve crop yield potentials. The yield potential of cereals such as rice, wheat, and sorghum has been successfully doubled through plant architecture modifications. Tall and traditional rice varieties have a yield potential of about 4 t per hectare and produced about 12–13 t of biomass per hectare. Of this, about 8 t is straw and the 4 t is grain which is a harvest index (HI) of 0.3 (Khush 2003). Improvements in the HI have been accomplished through the modification of the plant ideotype by reducing the plant height. This has been achieved through the incorporation of a recessive gene *sd1* that encodes gibberellin 20 oxidase and confers short stature (Khush 1999; Sasaki et al. 2002). The first short statured rice variety, IR8, was developed at the IRRI and produced a biomass of 18 t per hectare and a HI of 0.5. This equated to 9 t of grain per hectare. In addition to its semidwarf stature, IR8 also had other desirable traits such as profuse tillering, dark green and erect leaves for good canopy architecture, and sturdy stems (Chandler 1969).

To further increase the yield potential of rice, a new plant type has now been conceptualized (IRRI 1989; Khush 2005). Semidwarf rice varieties produce a large number of unproductive tillers and excessive leaf areas which cause mutual shading and a reduction in canopy photosynthesis. IRRI scientists have proposed further modifications to the plant architecture with low tillering (9–10 tillers for transplanted conditions): no unproductive tillers, 200–250 grains per panicle, dark green, thick and erect leaves, and a vigorous and deep root system. This proposed ideotype has become regarded as the "New Plant Type" (NPT) of rice. The objective has been to develop improved germplasm with 15–20% higher yield than the existing best varieties. In recent years, new genes and QTL have been identified which control these proposed traits for NPT varieties.

Control of Tillering

In rice, secondary tillers are produced from the primary tiller via the formation of lateral leaves and axillary buds. The axillary buds grow into tillers (Xing and Zhang 2010). The first secondary tiller is visible when the main culm has a fourth leaf and a secondary tiller comes out of the leaf sheath on the primary tiller. It is known that grain yield is mainly contributed by the primary tillers and early secondary tillers, while the late secondary and tertiary tillers make very little contribution to yield but will compete for nutrients. Hence, reducing axillary bud formation is desirable and will increase yield potential. In maize, the Teosinte Branched1 (TB1) protein is known to repress the growth of axillary organs (Doebley et al. 1997). Transgenic rice plants overexpressing OsTB1, the rice ortholog of maize TB1, show reduced lateral branching, while a loss-of-function mutant of OsTB1 exhibits enhanced lateral branching (Takeda et al. 2003). This indicates that OsTB1 functions as a negative regulator of lateral branching in rice.

Several low or high tiller mutants of rice have been isolated and characterized. The monoculm mutant *moc1* exhibits a defect in the formation of tiller buds. MOC1 belongs to a plant-specific GRAS family that functions to initiate axillary buds and promote their outgrowth (Li et al. 2003). In contrast, the rice mutants, *d3*, *htd1*, *d10*, *d14*, and *d27*, which have reduced plant heights, showed high tiller phenotypes. Interestingly, all causal genes for the high tiller mutants were found to encode proteins involved in the biosynthesis or signaling of strigolactones (SLs), a group of terpenoid lactones. These include D3, an F-box leucine rich-repeat (LRR) protein orthologous to *Arabidopsis* MEX2 (More Axillary Growth2) (Ishikawa et al. 2005); HTD1 (High-Tillering Dwarf1), the ortholog of *Arabidopsis* MEX3 (Zou et al. 2006); D10, a carotenoid cleavage dioxygenase 8 orthologous to MAX4 (Arite et al. 2007); D14, a member of the α/β-fold hydrolase superfamily (Arite et al. 2009); and D27, an iron-containing protein (Lin et al. 2009). Furthermore, the application of SLs inhibits shoot branching in these mutants, indicating that these proteins represent a new hormone class that regulates the above-ground architecture in rice (Umehara et al. 2008).

The rice *Fine Culm1* (*FC1*) gene causes an increased tillering phenotype and was found to be allelic to OsTB1 (Minakuchi et al. 2010). The *fc1* mutant is insensitive to a high dose treatment of GR24, a synthetic SL analog, implying that proper *FC1* function is required for the SLs to inhibit bud growth. The overexpression of *FC1* partially rescues the *d3* mutant tiller growth and plant height phenotype. Hence, *FC1/OsTB1* is suggested to partly function downstream of SL action.

Two research groups have cloned a QTL, *OsSPL14* that controls tiller number. They have demonstrated that increased levels of OsSPL14 results in rice plants with fewer tillers but more productive panicles and consequently higher grain yields (Jiao et al. 2010; Miura et al. 2010). These recently discovered genetic resources should prove useful in the future for developing high-yielding NPT varieties of rice.

Control of Grain Formation

Both the grain number per panicle and the grain weight are important traits for high yield varieties of rice. *Grain number1a* (*Gn1a*), a QTL that increases grain productivity in rice, was found to encode a cytokinin oxidase/dehydrogenase, previously named OsCKX2. Cytokinin oxidase/dehydrogenase is an enzyme that degrades the phytohormone cytokinin. The reduced expression of *Gn1a* causes cytokinin accumulation in inflorescence meristems and increases the number of spikelets, thus enhancing grain yield (Ashikari et al. 2005). Based on the grain number per plant, a 34% increase was found in the recessive *Gn1a* allele-carrying line compared with its controls.

The rice *lonely guy* (*log*) mutant produces a small panicle with a reduced number of branches and flowers. The *log* gene was found to encode a novel cytokinin-activating enzyme that functions in the final step of active cytokinin synthesis by directly converting inactive cytokinin nucleotides to their free-base forms via its cytokinin-specific phosphoribohydrolase activity. Its transcript is specifically localized within shoot meristem tips, thus contributing to the fine-tuning of the concentration and spatial distribution of bioactive cytokinins that is essential for regulating meristem activity (Kurakawa et al. 2007). These results further confirm that cytokinin is critical for the formation of the panicles in rice.

Grain weight is determined by the size and filling of the grain, and the regulation of grain size is controlled by both its length and width (Xing and Zhang 2010). Regarding the grain size, the rice gene *GS3*, a major QTL with minor effects on grain width and thickness, encodes a putative transmembrane protein with a PEBP-like domain, a TNFR/NGFR family cysteine-rich domain and a VWFC module. Sequence analysis has identified a nonsense mutation shared among all the large grain varieties in the *GS3* gene. This mutation causes a 178-amino acid truncation at the C terminus, suggesting that the *GS3* allele may function as a negative regulator of grain size (Fan et al. 2006).

GW2, a QTL that controls rice grain width, encodes a RING-type protein with E3 ubiquitin ligase activity that functions in protein degradation via the ubiquitin-proteasome pathway (Song et al. 2007). The *gw2* mutant shows an increased cell number, resulting in a wider spikelet hull and accelerated grain-filling rate. This suggests that GW2 negatively regulates cell division by targeting its substrate(s) to the proteasomes for regulated proteolysis. *qSW5*, a QTL involved in the determination of grain width in rice (also known as *GW5*) has been characterized in detail (Shomura et al. 2008). This study revealed that a deletion in *qSW5* results in a significant increase in sink size due to increased cell number in the glume of the spikelet (Shomura et al. 2008). *qSW5* encodes a novel protein of 144 amino acids (qSW5/GW5) that is localized

to the nucleus and that physically interacts with polyubiquitin in a yeast two-hybrid assay. These data suggest that both GW2 and qSW5 function in the ubiquitin-proteasome pathway to regulate cell division during seed development, possibly in the same pathway (Weng et al. 2008).

Grain-filling contributes greatly to grain weight. The rice *GIF1* (*Grain Incomplete Filling1*) gene (also referred to as *OsCIN2*) encodes a cell-wall invertase enzyme that hydrolyzes sucrose to glucose and fructose and which is involved in carbon partitioning during early grain filling. Ectopic overexpression of the cultivated *GIF1* allele with the 35S or rice Waxy promoter results in smaller grains, whereas *GIF1* expression driven by its native promoter increases grain production. Hence, a restricted expression pattern of the *GIF1* gene in cultivated rice compared with wild rice allele may be essential for grain filling (Wang et al. 2008).

Erect Leaves

It has been proposed that erect leaves that enhance light capture for photosynthesis and nitrogen storage for grain filling could increase grain yields in rice cultivars (Sinclair and Sheehy 1999). A rice brassinosteroid (BR)-deficient mutant, *Osdwarf4-1*, has an erect leaf phenotype that is associated with enhanced grain yields under dense planting conditions. *OsDwarf4* is a homolog of *Arabidopsis Dwarf4* encoding a cytochrome P450, CYP90B1 (Sakamoto et al. 2005). Molecular and biochemical studies have further revealed that two different cytochrome P450s, OsDwarf4 and D11, function redundantly in the rate-limiting step of BR biosynthesis. Hence, the *OsDwarf4* mutation alone causes only limited defects in BR biosynthesis and plant morphology.

The weakest allele of the rice *d61* mutants, *d61-7*, confers agronomically important traits including an erect leaf phenotype due to a loss of function of a BR receptor OsBRI1. The biomass of *d61-7* has been shown to be 35% higher than wild type at a high planting density. This indicates that *d61-7* more effectively assimilates biomass during reproductive organ development at a high planting density. Further, transgenic rice with only partial suppression of endogenous OsBRI1 produces about a 30% higher yield than wild type at a high planting density (Morinaka et al. 2006). In addition, antisense expression of OsBAK1, a coreceptor of OsBRI1, produces a desirable weak BR-insensitive mutant phenotype with erect leaves and normal reproduction (Li et al. 2009). These results demonstrate the feasibility of generating erect leaf rice plants by modifying BR synthesis or signaling.

Strong Root Systems

Roots are an important part of the plant architecture and are not only involved in foraging for water and nutrients but

also provide anchorage for the plant in soil. With a deep and thick root system, plants get better access to nutrients and water and show reduced lodging. The root-specific expression of the *OsNAC10*, a rice NAC (No Apical Meristem), *ATAF1-2*, and *CUC2* (Cup-Shaped Cotyledon) gene, using the root-specific promoter *RCc3*, resulted in thicker roots (1.25-fold increase in root diameter) due to the enlarged stele, cortex, and epidermis. These transgenic rice plants also had an increased grain yield of 5–14% and 25–42% over the controls under normal and drought conditions, respectively (Jeong et al. 2010). These results clearly demonstrate that thick roots can enhance the yield potential of rice.

Upland rice varieties when grown with no irrigation usually have deeper roots than their lowland counterparts (Araki and Iijima 2005). Genetic analysis of a population derived from a cross between lowland and upland varieties with contrasting root development characteristics has identified a large number of QTLs. Further intensive data mining has identified 861 root development QTL-associated microsatellite markers. This work provides a good platform for the isolation of candidate genes for strong root traits in the future (Suryapriya et al. 2009).

Enhancement of Photosynthesis

Current research on the enhancement of photosynthetic efficiency in rice includes the delaying of leaf senescence and the engineering of the C_4 photosynthetic machinery.

Delaying of Leaf Senescence

In several crop species, the incorporation of a "stay green" trait has been a major achievement for breeders (Evans 1993). Genotypes with the stay green trait (slower senescence) show prolonged canopy photosynthesis and thus give higher yields. While the nonfunctional stay green trait retains leaf greenness without sustaining photosynthetic activity, the functional stay green trait delays leaf senescence, thus maintaining photosynthetic competence. The functional stay green trait is thus beneficial and desirable and can enhance grain yield in rice. A functional stay green rice mutant, SNU-SG1, has been isolated and shows a high grain yield. Molecular marker analyses have identified two QTLs that most influence the functional stay green ability (Yoo et al. 2007). Cloning of these QTLs should assist in our future understanding of the molecular basis for achieving sustained photosynthetic activity for longer periods.

Engineering of C_4 Rice

The differences in the solar energy use efficiency between C_3 and C_4 plants is nearly 50%. Engineering the C_4 photosynthetic machinery into C_3 rice strains is considered to be a key strategy for dramatically raising rice yields (Hibberd et al. 2008; Zhu et al. 2010a). All domesticated C_4 crops have the "Kranz" anatomy, and to achieve the goal of converting rice into a C_4 variety, it may be necessary to alter the leaf morphology so that it is similar to that of C_4 plants. While C_4 maize has a narrower vein spacing, C_3 rice has a wider vein spacing. The wild rice relatives, *Oryza barthii* and *Oryza australiensis* have a relatively narrower vein spacing compared with cultivated rice. Rice mutants with a decreased interveinal space may be utilized to introduce some of morphological features of the C_4 pathway. Alternatively, it would be valuable to examine the leaf morphology in C_3 rice strains that show an altered photosynthetic metabolism. For example, the induction of high levels of NADP-malic enzyme (NADP-ME), a component of the C_4 pathway, into rice has led to a reduced stacking of the thylakoids in chloroplasts (Takeuch et al. 2000). This indicates that an altered metabolite flux may cause an altered leaf morphology.

Molecular engineering strategies have also been employed to introduce the known biochemical components of C_4 into rice. For example, overexpression of the maize phosphoenolpyruvate carboxylase (PEPC) gene in rice has produced a two- to threefold higher activity of this enzyme than that in maize, and the enzyme itself accounted for up to 12% of the total leaf-soluble protein. The PEPC transgenic plants also exhibited reduced O_2 inhibition of photosynthesis. These results suggest a possible strategy for introducing the key biochemical component of the C_4 pathway of photosynthesis into C_3 plants (Ku et al. 1999; Matsuoka et al. 2001).

Systems biology research may also play a pivotal role in identifying key regulatory factors that control the essential C_4 biochemical and anatomical features required to achieve high photosynthetic efficiency in rice (Zhu et al. 2010b). As a contribution to this effort, we have identified the rice orthologs for five major enzymes involved in the C_4 photosynthetic pathway and generated a hypothetical C_4 pathway in rice by combining it with the Calvin cycle (Fig. 1). All genes were identified using the Gramene pathway tool, ricecyc (http://www.gramene.org/pathway/ricecyc.html) (Liang et al. 2008; Jung et al. 2008b, c). The expression comparison data from dark-grown versus light-grown rice seedlings were incorporated into our hypothetical pathway. The expression levels of genes encoding four components of the C_4 pathway were increased under dark conditions. These were PEPC (Os02g14770), pyruvate orthophosphate dikinase (PPDK; Os03g31750), NADP-ME (Os1g09320), and carbonic anhydrase (CA; Os09g28910). Interestingly, transcripts for NADP-malate dehydrogenase (MDH; Os08g44810), PEPC (Os08g27840) and CA (Os01g45274), accumulated under
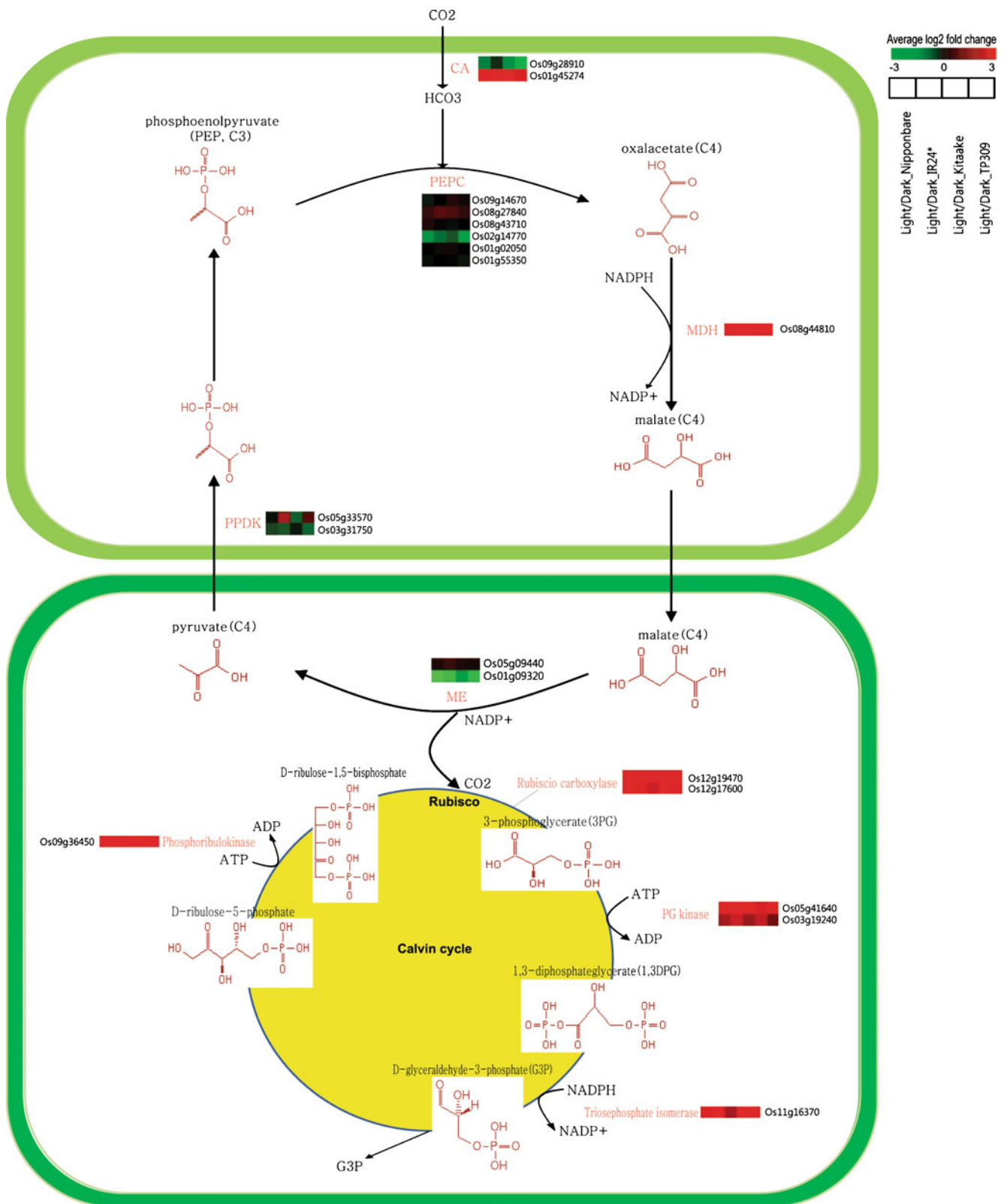
◄ Fig. 1 A hypothetical C_4 photosynthetic pathway in rice. The five components of the C_4 photosynthesis pathway in rice were identified from Plantcyc curated by Gramene. Four major components of the Calvin cycle were also selected. Rice microarray data for light- versus dark-grown seedlings of four rice varieties, Nipponbare, IR24, Kitaake and TP309, were integrated. IR24 is an *indica* cultivar and all others are *japonica*. *Red* in the heatmap indicates upregulation in light and *green* indicates downregulation. With regards to the C_4 photosynthesis pathway, carbonic anhydrase (CA) catalyzes the rapid conversion of CO_2 and H_2O to HCO_3^- and H^+; phosphoenolpyruvate carboxylase (PEPC) catalyzes the addition of CO_2 to phosphoenolpyruvate (PEP) to form the four-carbon compound oxaloacetate; NADP-malate dehydrogenase (MDH) catalyzes the conversion of oxaloacetate to malate; NADP-malic enzyme (NADP-ME) catalyzes the oxidative decarboxylation of L-malate, producing pyruvate, CO_2, and NADPH. In the Calvin cycle, Rubisco carboxylase catalyzes the first major step of carbon fixation; 3-phosphoglycerate kinase (PG kinase) catalyzes the transfer of a phosphate group from 1,3-biphosphoglycerate to ADP, forming ATP and 3-phosphoglycerate (PG); triosephosphate isomerase catalyzes the reversible interconversion of the triose phosphate isomers dihydroxyacetone phosphate and D-glyceraldehyde 3-phosphate; and phosphoribulokinase catalyzes the conversion of ATP and D-ribulose 5-phosphate to ADP and D-ribulose

light conditions. Transcripts for Calvin cycle components such as Rubisco carboxylase, 3-phosphoglyceric acid (PG) kinase, triose phosphate isomerase, and phosphoribulokinase, also accumulated largely under conditions of light. This analysis indicates that while all components of the C_4 pathway exist in rice, the expression pattern of some of the rice C_4 enzyme genes has become evolutionarily differentiated from that of the common C_4 genes. Hence, a strategy that involves the fine regulation of these components may shed new light on the possibility of engineering an efficient C_4 pathway in rice.

Prospects

The resources to allow systematic approaches to improve agronomically desirable traits are now available for rice. These include over 1,700 genome-wide transcriptome data, a protein–protein interaction network dataset, a web-based
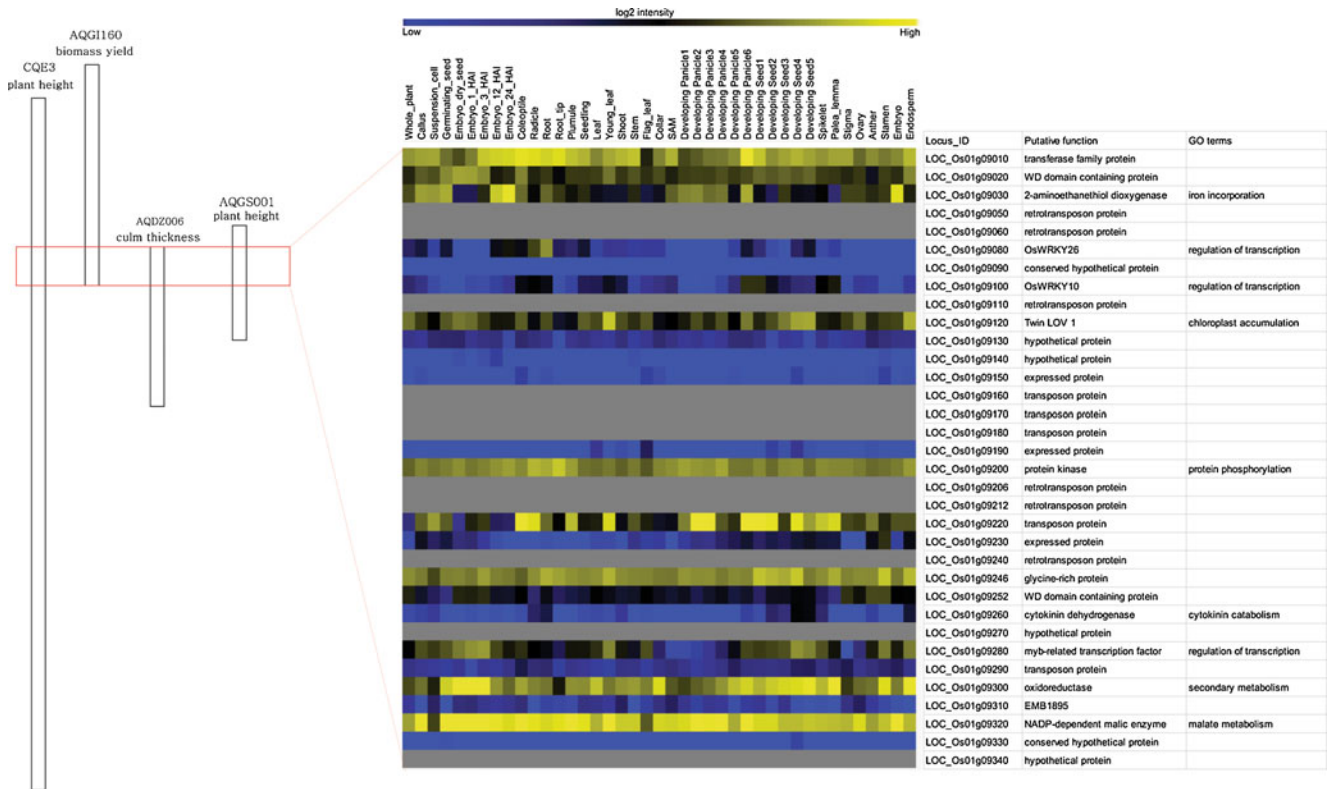

Fig. 2 In silico analysis to pinpoint the target regions associated with the QTLs related to biomass yield potential. The first step was to select the target QTLs associated with an important trait (i.e., biomass yield) by using the QTL database developed by Gramene. The second step involved the mapping of the QTLs to the gene loci. The third step was to identify overlapping regions among QTLs with similar features. The last step integrates multiomics data to the loci for the overlapping region. The GO terms were combined with anatomical gene expression data that had been reorganized by sorting about 830 Affymetrix gene chip results available from NCBI gene expression omnibus (GEO, http://www.ncbi.nlm.nih.gov/geo/) Plant Expression Database (PlexDB, http://www.plexdb.org/) and Arrayexpress (http://www.ebi.ac.uk/microarray-as/ae/). *SAM* shoot apical meristem, *Developing panicle 1* panicles of less than 3 cm in length, *Developing panicle 2* 3–5 cm, *Developing panicle 3* 5–10 cm, *Developing panicle 4* 10–15 cm, *Developing panicle 5* 15–22 cm, *Developing panicle 6* more than 22 cm, *Developing seed 1* 0–2 days post pollination (dap) seeds, *Developing seed 2* 3–4 dap seeds, *Developing seed 3* 5–10 dap seeds, *Developing seed 4* 11–20 dap seeds, *Developing seed 5*, 21–29 dap seeds

tool to integrate transcriptome or proteomic data into genome-wide metabolic pathways, and a large gene indexed mutant population (Liang et al. 2008; Jung et al. 2008a). Intensive phenotype datasets using these gene indexed mutant resources will soon also be accessible. Using these multiomic resources, it has now become possible to select the key components responsible for desirable traits to improve rice yields. To date, information on over 8,600 rice QTLs has also been collected and curated by the database "Gramene" (Ni et al. 2009). Hence, in silico QTL analysis, combined with genome-wide omics data, will help pinpoint the target regions associated with the rice QTLs of interest by exploring the loci that are enriched by similar traits. A future strategy for the in silico analysis of a QTL associated with biomass yield potential is shown in Fig. 2. The four QTLs previously identified as CQE3 (plant height), AQC1160 (biomass yield), AQDZ006 (Culm thickness), and AQGS001 (plant height), respectively, share a target region containing 34 genes on rice Chromosome 1. Interestingly, this region includes a gene (Os01g09320) encoding NADP-ME which is a key component of C_4 photosynthesis. In gene expression profiles of 42 anatomical samples collected from a public microarray database, the NADP-ME gene shows high expression in most cases. This suggests that the gene is a strong candidate for a biomass yield QTL, although this has not been confirmed as yet. It will be of great value in the future to develop a database that integrates rice QTLs into an all multiomics dataset. Finally, this well-integrated resource should help identify novel components that can be utilized to generate higher yielding rice varieties.

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