EDITORIAL: REFLECTIONS ON THE PLANT CELL CLASSICS

Understanding the Molecular Bases of Agronomic Trait Improvement in Rice

Increasing crop yield is a major challenge for agricultural scientists because of an ever increasing world population and a finite amount of arable land. Rice is a staple food feeding over half of the world’s population. During the last two decades, tremendous progress has been made in understanding molecular mechanisms underlying important agronomic traits, and The Plant Cell has made an extraordinary contribution in these advances to broaden and deepen our understanding of rice growth and development, thus facilitating the improvement of rice grain yield through molecular breeding. Here, we reflect on five of these important papers, published in the decade from 2000-2009, that provided critical advances in our understanding of heading date, plant height, heterosis, and mechanical strength, all of which are vital for rice production.

Heading date or flowering time is a critical trait for a crop to achieve high yield through making maximum use of sunlight and temperature. In rice, a short-day (SD) plant for which flowering is promoted by SD conditions, heading date shows a wide range of variation among rice cultivars and is regulated mainly by genes controlling photoperiod sensitivity. At the beginning of the 21st century, many quantitative trait loci (QTLs) had been isolated using segregating populations derived from crosses between different background cultivars, varieties, or subspecies. However, the allelic relationships among these QTLs/genes and their precise positions in the genome remained elusive. More importantly, extremely limited regulatory mechanisms had been elucidated, owing to a lack of molecular information of the involved genes. A breakthrough was made in 2000, when Yano et al. reported the cloning of the QTL Heading date 1 (Hd1) in the segregating populations of Nipponbare (ssp. japonica) and Kasalath (ssp. indica) through a map-based approach using more than 9,000 BC3F3 lines (Yano et al., 2000).

Hd1 was found to encode a homolog of Arabidopsis CONSTANS (CO) and to promote heading under the SD photoperiod while repressing heading under long-day length (LD) conditions in rice. In Arabidopsis thaliana, a long-day (LD) plant, CO is a key regulator of floral promotion under LD conditions and activates the expression of FT, an Arabidopsis florigen gene. In rice, Hd1 is a major determinant of natural variation and its expression was not largely affected by a change in day length. Yano et al. (2000) provided an excellent example of map-based cloning of QTLs and opened a new era in understanding the genetic basis of complex agronomic traits in rice and other crops. Using this strategy many other genes controlling heading date have now been identified from natural variations or rice mutants. These studies have greatly improved understanding of the gene regulatory network for flowering time in rice.

Plant height and tiller number also contribute significantly to crop production and agricultural practices. The phytohormone gibberellins (GAs) play important roles in stem elongation, seed germination, and flower development. The adoption of semidwarf alleles affecting GA biosynthesis or signaling, which greatly improved lodging resistance and grain yield of cereals, led to the “Green Revolution” of record yield increases throughout Asia after the 1960s. Although a series of mutants with altered GA levels or GA response were identified from dicot and monocot plants about two decades ago, how the GA signal is transduced into morphologic and biochemical changes in plants remained largely unknown for a long time. In 2001, Ikeda et al. reported a recessive rice mutant slender (slr1-1), which was much taller than wild type and insensitive to exogenously applied uniconazole, an inhibitor of GA biosynthesis. The slr1-1 mutant was shown to be a constitutive GA response mutant, and molecular cloning further showed that SLR1 encodes OsGAI, which is homologous to Reduced Height (RHT) in wheat, D8 in maize and GA-INSENSITIVE (GAI) and RGA in Arabidopsis (Ikeda et al., 2001). The wheat green-revolution gene RHT-B1 and RHT-D1 are gain-of-function alleles caused by an N-terminal truncation near the DELLA domain. Even though wheat has a hexaploid genome, these dominant alleles still cause obvious dwarf phenotypes in the variety Norin 10 and its hybrid progenies. Soon after this research, the SEMIDWARF1 (SD1) gene responsible for green revolution in rice was isolated and characterized to encode a GA20ox isoenzyme (GA20ox-1) that catalyze the conversion of GA3 to GA20 (Spielmeyer et al., 2002; Sasaki et al., 2002). Genetic and functional analyses of SLR1/RHT and SD1 in rice and wheat have greatly improved the understanding of the biosynthesis and signalling pathways of GA and provide a powerful strategy to manipulate plant height of important crops.

Tiller development determines panicle number, thus directly influencing crop yield. Tilling is also an ideal model system for elucidating molecular mechanisms of lateral bud development. Strigolactones (SLs) are carotenoid-derived signaling molecules that are transported from root to shoot and repress bud outgrowth in flowering plants. In 2008, SLs were characterized as a new type of phytohormone that are deficient in classical dwarf and high tillering mutants d10 and d17, while accumulated in the signaling mutant d3. The D17 and D10 genes encode the carotenoid cleavage dioxygenase 7 (CCD7) and CCD8 in rice. However, the SL biosynthesis and signaling pathways still remained to be elucidated. In 2009, Lin et al. reported the cloning and characterization of the high tilling and dwarf mutant d27, which displayed enhanced and accelerated tiller bud outgrowth and increased polar auxin transport. D27 encodes an iron-containing protein that was localized in chloroplasts. More importantly, D27 was predominantly expressed in young leaves, axillary buds, inflorescence...
promodia, lateral and crown roots and was required for SL biosynthesis, indicating that D27 is a novel enzyme in SL biosynthesis pathway (Lin et al., 2009). Subsequent studies found that D27 catalyzes an isomerization of all-trans-β-carotene to 9-cis-β-carotene, which is the first step of SL biosynthesis in dicots and monocots.

Heterosis or hybrid vigor is the tendency of hybrid offspring to exhibit increased vigor and productivity over their parents. Exploitation of heterosis in maize and rice has greatly increased grain yield. However, hybrid sterility is a bottleneck in the utilization of strong heterosis. Cytoplasmic male sterility (CMS) and nucleus-controlled fertility restoration (FR) are widespread plant reproductive features that provide useful tools to exploit heterosis in crops. In 2006, Wang et al. cloned genes responsible for the CMS-BT (Boro II type) system, and elucidated molecular mechanism underlying the gametophytic CMS/RF system. The CMS-BT mitochondrial genome contains a chimeric open reading frame orf79, which encodes a cytotoxic polypeptide and whose preferential accumulation in microspores causes male sterility. The Rf-1 locus contains two closely linked genes, Rf1a and Rf1b, which encode PPR proteins. Rf1A and Rf1B target to mitochondria to destruct orf79 mRNA by different post-transcriptional mechanisms. However, in the presence of both restorers, Rf1a is epistatic to Rf1b. Moreover, Rf1a has a role on enhancing the editing of atp6 mRNA as its primary function (Wang et al., 2006). This study provided critical insight into the CMS/RF interaction at the molecular level and the mechanism of cytoplasmic-nuclear interaction. More importantly, valuable orf79 variants were identified and employed to develop new rice CMS lines, making a great contribution to hybrid seed production in China.

Plant mechanical strength is another important agronomic trait that sets the basis of lodging resistance and also the usefulness of cereal straws as animal forage. The rice brittle culm (bc) mutants provided an excellent resource to investigate the mechanisms regulating mechanical strength of the plant body and biosynthesis of plant cell walls. However, the responsible genes and mechanisms regulating mechanical strength were elusive. In 2003, Li et al. reported the reduced mechanical properties and altered cell wall composition of the rice bc1 mutant and identified BC1 gene through map-based cloning. BC1 is expressed mainly in developing sclerenchyma cells and in vascular bundles of rice. BC1 is a COBRA-like protein that functions in regulating the biosynthesis of secondary cell walls to provide the main mechanical strength for rice plants (Li et al., 2003). This work cloned the first gene controlling mechanical strength in rice and opened the gate for improving plant cell wall biosynthesis in crops through molecular assisted breeding.

These pioneering papers opened up a new era of exploring the mechanisms underlying complex agronomic traits in crops at the molecular level. Importantly, these findings further promote the rational design of these agronomic traits and the cultivation of elite crop varieties with high yield, robust environmental adaptation, superior lodging resistance, and strong hybrid vigor through molecular breeding.

**REFERENCES**


