

REVIEW

Genetic modification of plant architecture and variety improvement in rice

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The structure of the aerial part of a plant, referred to as plant architecture, is subject to strict genetic control, and grain production in cereal crops is governed by an array of agronomic traits. Rice is one of the most important cereal crops and is also a model plant for molecular biological research. Recently, significant progress has been made in isolating and collecting rice mutants that exhibit altered plant architecture. In this article we summarize the recent progress

in understanding the basic patterning mechanisms involved in the regulation of tillering (branching) pattern, stem structure and leaf arrangement in rice plants. We discuss the relationship between the genetic modification of plant architecture and the improvement of pivotal agronomic traits in rice.

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Introduction

Plant architecture is the three-dimensional organization of the part of a plant that is above ground. It encompasses branching (tillering) pattern, plant height, the arrangement of leaves and the structure of reproductive organs. Plant architecture is of major agronomic importance as it determines the adaptability of a plant to cultivation, its harvest index and potential grain yield (Reinhardt and Kuhlemeier, 2002). Since the late 1960s, global production of cereal grains has doubled owing to the great success of the Green Revolution, which created high-yielding cultivars with shorter and sturdier stems in rice and wheat by the modification of plant architecture (Khush, 2001).

Rice (*Oryza sativa*), one of the dominant grain crops, feeds more than half the world's population. In most developing countries, the demand for rice will increase dramatically with population growth. To meet this challenge, new elite varieties of rice, with a plant architecture that can produce much higher grain yield, need to be developed (Yuan, 1997; Khush, 2001). An understanding of the mechanisms that control the plant architecture of rice will facilitate the breeding of rice varieties with higher yield potentials.

Rice is an annual grass crop with round, hollow and jointed culms (stems). The developmental course of rice is roughly divisible into two stages: a vegetative stage and a reproductive stage. The vegetative stage is usually longer and consists of repeated formation of a number of leaves and branched tillers as lateral organs. Little internode elongation in rice occurs during the vegetative

stage. After producing 10 or more foliage leaves, rice plants enter the reproductive stage, during which rapid elongation of internodes occurs between the last 4–6 leaf nodes (Li, 1979). On transition to the reproductive stage, every tiller may generate an inflorescence called a panicle, which is borne on the uppermost internode of the culm. The panicle bears rice spikelets that develop into grains. Normally, a mature rice plant has a main culm and a number of side tillers.

In genetic improvement of rice, several genetic traits are selected to increase yield potential, yield stability and wide-scale adaptability (Khush, 2001). The grain yield of rice plants consists of three main components—number of panicles per unit area, number of spikelets per panicle and kernel weight (Peng *et al.*, 2000). These components contribute to grain yield to differing extents and their contributions vary with genotype, environmental conditions and cultivation practice. However, plant architecture may be the most important factor affecting grain yield in rice. Rice plant architecture is mainly determined by tiller pattern, plant height, leaf shape and arrangement, and panicle architecture.

In this article we review the latest advances in the identification and characterization of genes involved in the control of vegetative organs, including those that control shoot branching (tillering), plant height and leaf arrangement, and briefly discuss the potential to use these advances in the genetic improvement of rice.

Control of rice tillering

Shoot branching is a fundamental component of plant architecture. Characteristics of shoot branching are type and degree, or pattern, and angle, which determines the amount of space occupied by the branches. Among the species of grasses that have been domesticated to cereal crops there are two distinct types of vegetative branching: tiller and axillary. In tiller branching, the axillary

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meristems (AMs) form at the basal nodes of the grass culm (main stem) and grow out to form side tillers that are similar in shape and height to the main culm. In axillary branching, axillary branches are produced from axillary buds at higher nodes of the culms, where culm internodes have expanded. Branching angle may result in an upright growth habit, or variously decumbent (stoloniferous or rhizomatous) growth habit.

The vegetative branched shoot in rice plants is called a tiller. Shoot branching, or tillering, is a crucial agronomic trait that is directly linked to the number of panicles, which in turn is one of the most important determinants of grain yield. The rice AMs (tiller buds) located at the first few nodes of the culm grow out and elongate to become tillers. The majority of the side tillers emerge at ground level, producing their own adventitious roots and achieving at least partial independence from the main shoot. The axillary buds produced at higher nodes of the culm, where culm internodes have expanded, remain dormant when the panicle of the main culm begins to differentiate. The branched tillers undergo two distinct steps: initiation of a new AM at the axil of a leaf and outgrowth of the axillary buds. The characterization of mutants defective in AM initiation and/or outgrowth in various plants has provided opportunities to examine the process of shoot branching.

Mutants that are impaired during AM initiation have been characterized in rice. The *moc1* mutant produces a main culm with no or limited side tillers (Figure 1a) as well as a reduced number of rachis branches and spikelets (Li *et al.*, 2003). The *moc1* gene was isolated using map-based cloning. Sequence analyses indicate that *MOC1* is a

rice ortholog of the tomato *LS* and *Arabidopsis LAS* gene (Li *et al.*, 2003), which encode putative transcriptional regulators of the plant-specific GRAS family (Bolle, 2004). The similarity of the *Ls/LAS/MOC1* mutant phenotypes and transcomplementation experiments indicate that these genes are conserved over large evolutionary distances. The expression of the early meristem marker gene *OSH1* was abolished in the axillary regions of the mutant *moc1*, where lateral meristems were initiated in wild-type plants (Li *et al.*, 2003). These findings suggest that the gene *MOC1* is involved at an early step in the pathway leading to lateral meristem formation, probably ensuring that the meristematic character of leaf axil cells is retained until AM formation. Although the mechanism of regulation of the gene *MOC1* expression and the target gene of the transcription factor *MOC1* are not known, data from Li *et al.* (2003) suggest that *MOC1* is a key regulator leading to AM initiation.

The growth of axillary buds into side shoots is influenced mainly by hormonal signals. For example, isolation and characterization of the *Arabidopsis* genes more axillary growth (*MAX*) suggest that a novel regulatory pathway involving carotenoid-derived signaling molecules controls the growth of axillary buds (Sorefan *et al.*, 2003; Booker *et al.*, 2004; Bouvier *et al.*, 2005; Bennett *et al.*, 2006). *MAX1* encodes a member of the CYP450 family and acts downstream of *MAX3* and *MAX4* in the biosynthesis of the branching signal (Booker *et al.*, 2005). *MAX3* and *MAX4* encode divergent carotenoid cleavage dioxygenase and are required for synthesis of a carotenoid-derived long-range signal in the control of shoot branching (Booker *et al.*, 2004). *MAX2*

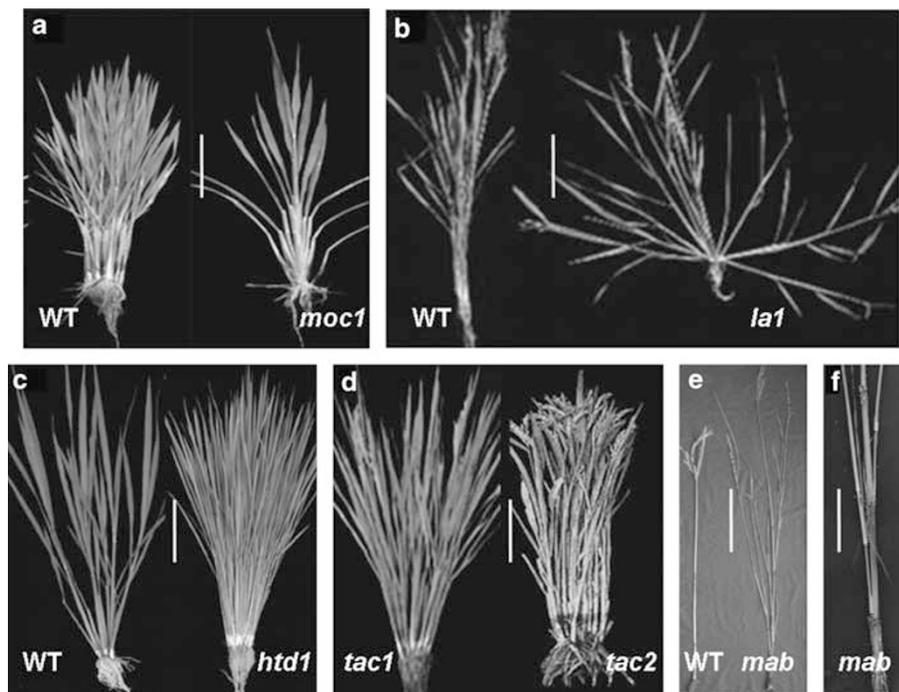


Figure 1 The different phenotypes of tillering (branching) mutants in rice. Mutations in branching pattern result in changes in the number of tillers, the position of tiller initiation or tiller angle. (a) The *moc1* mutant plant with one culm (right) and its wild type (left) at maximum tillering stage (according to Li *et al.*, 2003). Bar, 8.1 cm. (b) The *la* mutant plant with a spreading phenotype in growth habit (right) and its wild type at the mature stage (left) (according to Li *et al.*, 2007). Bar, 26.9 cm. (c) The *htd1* mutant plant with excessive tillers (right) and its wild type (left) at the maximum tillering stage (according to Zou *et al.*, 2005). Bar, 8.5 cm. (d) The whole plant with different tiller angles at the heading stage (according to Yu *et al.*, 2007). Bar, 28.1 cm. (e) The *mab* mutant plant with an axillary branching pattern (right) and its wild type (left) at reproductive growth stage. Bar, 29 cm. (f) The magnification of the axillary branches on higher culm having adventitious roots. Bar, 1.8 cm.

encodes an F-box protein that is a member of the SCF family of ubiquitin ligases, which have been suggested to have a role in the perception of the *MAX1*-, *MAX3*- and *MAX4*-dependent signals in the stem (Bennett *et al.*, 2006). Although a rice mutant corresponding to *Arabidopsis max1* has not yet been identified, all other corresponding mutant phenotypes in rice are similar to the *Arabidopsis* mutants in having an increased number of tillers and reduced height. The functional homologs of *MAX2*, *MAX3* and *MAX4* have been identified in rice (Ishikawa *et al.*, 2005; Zou *et al.*, 2005; Arite *et al.*, 2007). For instance, the phenotypes of the *htd1* mutant are similar to the *max3* mutant in *Arabidopsis* (Figure 1c). The gene *HTD1* encodes a rice ortholog of *Arabidopsis MAX3* (Zou *et al.*, 2005), indicating that the *MAX3/HTD1* orthologs in function were conservation. These data indicate that carotenoid-derived compounds are vital components of the novel hormone signaling pathway for controlling tiller formation in rice and suggest that this novel regulatory pathway controlling shoot branching is likely to be conserved from dicotyledonous to monocotyledonous plants.

Tiller angle—the angle between the main culm and its side tillers in grass—is another feature of plant architecture that contributes to the agronomic performance of rice (Xu *et al.*, 1998). Recently, the rice gene *TAC*, which controls the size of the tiller angle (Figure 1d), was cloned and encodes a small protein (259 a.a.) of unknown function. Rice transformation experiments confirm that high expression of the gene *TAC1* results in a wider tiller angle whereas low expression leads to erect tillers with a smaller tiller angle (Yu *et al.*, 2007).

Domesticated varieties are less branched than their wild relatives in most crops, allowing closer planting and less self-shading (Doust, 2007). Normally, elite rice plants do not have axillary branches in the axils of leaves higher up the culms, where the stem internodes have elongated. Recently, we identified a novel rice mutant having more axillary branches (*mab*) at the upper nodes, where the internodes are elongated and adventitious roots are produced (Figures 1e and f). The mutant also produces fewer tillers at the basal nodes, where the stem internodes are non-expanded, and primary branches with crown roots at the nodes where internodes elongated (Figure 1f). The *mab* mutant has a longer life cycle compared with the wild type and produces secondary branches that originate from the primary branches. The *MAB* gene has been cloned through map-based cloning and encodes a novel protein (Hwa *et al.*, unpublished data). Investigation of its functions in controlling the axillary branches from the upper nodes is under way. Another tiller mutant, *la*, was identified (Figure 1b). The *la* gene product is a novel, grass-specific protein (Li *et al.*, 2007). The *la* mutant is an extremely spreading phenotype with a creeping growth habit, and thus occupies a large amount of space. *Oryza rufipogon* and *Oryza longistaminata* are two wild relatives of cultivated rice. The variation of tillers or branches of perennial *O. rufipogon* is from vertical to creep, depending on water condition and altitude in their microhabitats (Gao *et al.*, 2000). *O. longistaminata* is a perennial with creeping, branched rhizomes. The *mab* mutant is similar to *O. rufipogon* in branching pattern and the *la* mutants is similar to *O. longistaminata* in creeping growth habit, suggesting that there were dramatic morphological

changes in cultivated rice during evolution from its wild progenitor. Mutations of key loci leading to striking evolutionary changes have been reported in several plants, including the gene *tb1* that governs the fate of the AMs in maize and distinguishes cultivated maize (*Zea mays* L. ssp. *mays*) from its probable wild progenitor (*Z. mays* ssp. *parviglumis*; Hu *et al.*, 2003). Molecular analysis of the rice *mab* and *la* genes will contribute significantly to our understanding of the evolutionary history of the domesticated crops of grass family.

Control of plant height in rice

Plant height is not only a decisive factor in plant architecture, but also an important agronomic trait that is directly linked to the harvest index and yield potential. The total number of elongated internodes and the length of each elongated internode determine plant height. A rice plant usually has 4–6 elongated internodes and its height is mediated by qualitative genes and quantitative trait loci (QTL; Huang *et al.*, 1996), and influenced by environmental factors.

Numerous data from mutants indicate that the pattern of internode elongation, which determines the height of rice plant, is regulated in two different ways: the genes controlling internode elongation either express in all internodes, allowing coordinated elongation of every internode, or the genes act only one or two internodes. The genes encoding gibberellic acid (GA) and brassinosteroid (BR) biosynthetic or signaling pathways have been identified using dwarf mutants of rice, and were found to act at all elongated internodes. The *semi-dwarf* (*sd-1*) 'Green Revolution' allele in rice (Figure 2b) is a recessive loss-of-function mutation in one of the major GA biosynthetic genes, *GA20-oxidase* (*GA20ox*). It differs from the Green Revolution wheat *Rht-B1/Rht-D1*, in which the GA signaling pathway is impaired (Sasaki *et al.*, 2002; Spielmeier *et al.*, 2002; Oikawa *et al.*, 2004). Loss-of-function mutations in the *GA20ox* and *GA3ox* genes or overexpression of the gene *GA2ox* have a dwarfing effect (Sakamoto *et al.*, 2001). In contrast, the *slender rice* (*slr1*) plant was found to be a constitutive GA-responsive mutant that was much taller at the seedling stage than the wild-type plant (Ikeda *et al.*, 2001). The *SLR* gene product is an ortholog of *GAI* and *RGA* in *Arabidopsis*, *RHT* in wheat, and *D8* in maize, and functions negatively in the GA signal transduction pathway mediated by the DELLA domain (Peng *et al.*, 1997; Ikeda *et al.*, 2001). *DWARF1* (*D1*) in rice is the only gene that encodes an α -subunit of the heterotrimeric G protein (Ashikari *et al.*, 1999), and the mutant *d1* has reduced stature and dark green leaves, similar to GA-deficient rice plants. The first leaf of the mutant *d1* plants is GA-insensitive, but the second leaf shows a normal GA response. Loss-of-function mutations in the *Arabidopsis* ortholog do not produce the dwarf phenotypes observed in rice (Ullah *et al.*, 2001). The normal GA sensitivity of the second leaf in rice and the lack of dwarf phenotype in *Arabidopsis* suggest that *D1* protein may not be directly involved in GA signaling.

Another classic rice dwarf mutant, *d2*, was characterized as a BR-deficient mutant (Hong *et al.*, 2003). *D2* encodes a new member of the cytochrome P450 family, CYP90D2, which is highly homologous to a BR biosynthetic enzyme that catalyzes the reactions from

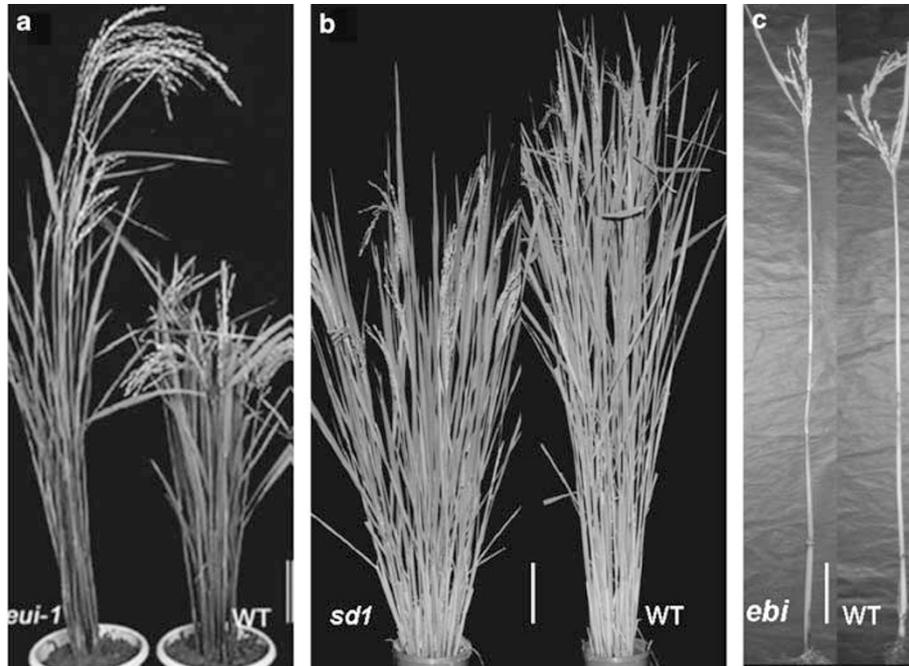


Figure 2 The different phenotypes of plant height mutants in rice. The figure shows three different patterns of internode elongation that are regulated by different types of genes. (a) Elongated uppermost internode mutant *eui* with a longer uppermost internode (left) and its wild type after heading (right; according to Zhu *et al.*, 2006). Bar, 20.7 cm. (b) Semi-dwarf mutant *sd1* with short stem by decreasing length of each internode (left) and wild-type plants (right). Bar, 14.2 cm. (c) Elongated basal internode mutant *ebi* with special longer basal internode (left) and its wild type (right). Bar, 14.5 cm.

6-deoxoteasterone to 3-dehydro-6-deoxoteasterone. Recently, a new cytochrome, P450 (CYP724B1), was isolated in rice and characterized as a homolog of the enzyme involved in BR biosynthesis (Tanabe *et al.*, 2005). The loss-of-function mutation of this enzyme resulted in a rice dwarf mutant, *dwarf11* (*d11*). Another rice mutant *d61*, less sensitive to BR compared to the wild-type plant, is defective in internode elongation and lamina joint bending (Yamamuro *et al.*, 2000). Molecular analysis reveals that the gene *D61* encodes OsBRI1 protein, a homolog of the *Arabidopsis* BRI1 protein, indicating that the OsBRI1 mediates the BR signaling pathway in rice, which can regulate internode elongation and lamina joint bending.

Although a large number of rice dwarf mutants have been characterized, few of them have been successfully applied to improve rice varieties owing to their severe dwarfism and sterility (Spielmeyer *et al.*, 2002). However, it has been shown that the rice *GA 2-oxidase* gene fused to the promoter of the rice *OsGA3 ox2* gene, which expresses mainly in vegetative tissue transferred into rice, can confer the dwarf phenotype without affecting other economic traits (Sakamoto *et al.*, 2003). RNAi suppression of the *OsGA20ox* gene in rice also results in semi-dwarf plants without altering other related traits (Qiao *et al.*, 2007).

Recently, two different genes, elongated uppermost internode (*eui*) and elongated basal internode (*ebi*), which both affect internode elongation, have been identified in rice. The *eui* mutant (Figure 2a) has been used in hybrid rice seed production to eliminate the panicle enclosure of male sterile cultivars. The *EUI* gene encodes a cytochrome P450 mono-oxygenase, CYP714D1, which is expressed mainly in the divisional zones of internodes

and reduces the levels of bioactive gibberellin GA4. The *eui* mutant exhibits an extreme accumulation of GA4 and GA1, which promote cell elongation in the uppermost internodes (Zhu *et al.*, 2006). Overexpression or down-regulation of *EUI* in rice plants gives rise to dwarf or *eui*-like transgenic plants, respectively, suggesting its potential application in the genetic modification of hybrid rice. The *ebi* mutant has two elongated basal internodes at the basal nodes of main culm (Figure 2c). The gene *EBI* has been isolated through map-based cloning and encodes a novel protein (Hwa *et al.*, unpublished data). Investigation of its functions in controlling internode elongation is under way.

A number of major QTL that affect the height of rice plants in a developmental stage-specific manner have been identified using conditional QTL mapping approaches (Yan *et al.*, 1998). Recently, a QTL, *Ghd7*, which encodes a CCT domain protein, was isolated from an elite rice hybrid. *Ghd7* transgene-positive plants have a longer uppermost internode and thicker stems than their transgene-negative counterparts. The increased height of *Ghd7*-positive plants is a result of their increased cell number of culms (Xue *et al.*, 2008).

It is well known that rice plant height is a strong negatively correlation with tiller number (Hong *et al.*, 2003; Ishikawa *et al.*, 2005). A similar phenomenon is found in *Arabidopsis max* and pea *rms* mutants (Sorefan *et al.*, 2003; Booker *et al.*, 2004). However, the molecular mechanisms that underlie the cross talk between plant height and branching are poorly understood. The finding that transgenic rice plants harboring *MOC1* gene and the *htd1* mutants are dwarf but produce more tillers than wild-type plants (Li *et al.*, 2003; Zou *et al.*, 2006) provides good opportunity to investigate the genetic control network.

Control of leaf development in rice

Leaves are often the most noticeable parts of a plant; they are the predominant photosynthetic organs and are of pivotal importance for carbon fixation. Some leaf parameters, such as shape, number, size, thickness, direction and chloroplast level are very important factors influencing the biomass formation and success of a plant. In this section we briefly introduce the genes that regulate leaf development and the direction of the top three functional leaves, which are main contributors to grain yield in rice.

A prototypical leaf has three axes: proximodistal (tip–base), dorsiventral (adaxial–abaxial) and lateral (left–right; Champagne and Sinha, 2004; Reinhardt and Kuhlemeier, 2002). As with most grass leaves, rice leaves are clearly divided into the proximal sheath and the distal blade. Leaf blade length is controlled by proximodistal axis. In *Arabidopsis*, leaf length is specifically mediated by the number of leaf cells by the ROT4 peptide (Narita *et al.*, 2004). The genome of *Arabidopsis* contains 22 homologs of ROT4, which encodes a small protein containing 53 amino acids. As the ROT FOUR-LIKE (RTFL) genes are short, most members, including ROT4 itself, are non-annotated. All members of the RTFL family include a conserved 29-amino acid domain, called the RTF domain, and are rich in basic amino acids. Overexpression of the ROT4 RTF domain alone in *Arabidopsis* is sufficient to decrease leaf length (Narita *et al.*, 2004). The rice genome includes 23 members of RTFL gene family (Tsukaya, 2005). The organogenesis of leaves in rice is highly dependent on cell proliferation in the longitudinal direction. Expression analysis of the RTFL genes in rice will contribute to a better understanding of the molecular mechanism of leaf development in proximodistal axis direction.

The adaxial–abaxial or dorsiventral axis determines asymmetric development of leaves, resulting in the development of the specialized adaxial surface for light capture and the abaxial surface for gas exchange. Several genes are involved in the development of the dorsiventral axis in *Arabidopsis*. The class III homeodomain leucine zipper (HD-ZIPIII) genes *REVOLUTA* (*REV*), *PHABULOSA* (*PHB*) and *PHAVOLUTA* (*PHV*) are responsible for adaxialization (McConnell *et al.*, 2001; Emery *et al.*, 2003), whereas the *KANADI* (*KAN*) and *YABBY* (*YAB*) gene families are responsible for abaxia-

lization (Eshed *et al.*, 2001; Kerstetter *et al.*, 2001). Analysis of the rolled-leaf mutants in maize shows that the role of HD-ZIPIII in adaxial specification is conserved between monocots and eudicots. Juarez *et al.* (2004a) have demonstrated that the maize ortholog of the *revoluta* gene, *Rld1*, was misexpression in the semi-dominant mutant *Rld1-Original* (*Rld1-O*), which results from a single nucleotide substitution in the miRNA166 complementary site.

The *YAB* gene family encodes YABBY proteins containing a zinc-finger and a helix-loop-helic domain and may function as a transcriptional factor. *KAN* gene family encodes Golden2/*Arabidopsis* response-regulated/Psr1 (GARP) transcription factors. Both *YABs* and *KANs* are small gene families and *KAN* proteins are likely to repress adaxial-promoting HD-ZIPIII that repress expression of the *KAN* and *YAB* genes (Eshed *et al.*, 2001, 2004). This mutually antagonistic relationship between *KAN* and HD-ZIPIII appears to drive lamina growth that is dependent on the activity of the *YAB* proteins. In maize, two *YABBY* genes are expressed on the adaxial side of the leaf, suggesting that *YABBY* genes may direct lateral outgrowth rather than determine cell fate (Juarez *et al.*, 2004b). Consistent with this view, mutations in the rice *YABBY* gene *DROOPING LEAF* resulted in defects in midrib formation, possibly owing to reduced cell division (Yamaguchi *et al.*, 2004). Cosuppression of the *YABBY* transcription factor *YAB1* expression induces a rolled-leaf phenotype, but the midrib seems to be normal (Dai *et al.*, 2007). The *YAB1* plants at the heading stage produce droopy leaves, forming an acute angle with the sheaths (Figures 3a and b). These results indicate that the expression patterns of *YABBY* family transcription factors, and possibly their function, may have diverged during evolution.

Small RNAs are important regulators of gene expression. The precise expression pattern of HD-ZIPIII protein in the adaxialization pathway is controlled by microRNAs (miRNA165 and miRNA166) in *Arabidopsis* (Emery *et al.*, 2003). In maize, adaxial/abaxial leaf polarity is established by an abaxial gradient of miR166, which spatially restricts the expression of the HD-ZIPIII transcription factors that specify adaxial/upper fate. *ARGONAUTE1* (*AGO1*), a component of the RNA silencing machinery, is also required for dorsoventrality of leaves by the proper regulation of miRNA165/166, which targets the

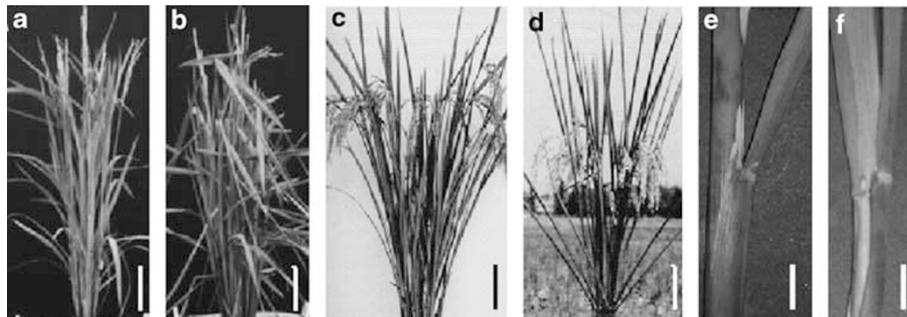


Figure 3 Leaf arrangements of different mutants in rice. (a) Leaves of wild-type rice plant at the heading stage. Bar, 15.8 cm. (b) Coexpression of *YAB1*-inducing rolled leaves at the heading stage, forming an acute angle with the sheaths (according to Dai *et al.*, 2007). Bar, 15.8 cm. (c) Improved high-yielding plant having semi-dwarf stature and a slightly larger leaf angle. Bar, 16.4 cm. (d) Ideotype plant with moderate tillering, erect and rolled leaves, and the top three functional leaves above the panicle. Bar, 17.0 cm. (e) Leaf of wild-type rice having an acute leaf angle. Bar, 1.1 cm. (f) Erect-leaf phenotype of super high-yielding rice variety. The degree of bending between leaf blade and sheath of the super rice is less than that of the wild type.

cleavage of the HD-ZIPIII mRNAs (Kidner and Martienssen, 2004). There are at least 18 members of the AGO family in rice (Shi *et al.*, 2007). One rolled-leaf gene, *RL(t)*, belonging to the *Argonaute* (AGO) family, is located to a region of about 137 kb on the long arm of chromosome 2 of rice (Shao *et al.*, 2005). Shi *et al.* (2007) recently reported that *OsAGO7*, a member of the rice AGO gene family, encodes a 1048 amino acid protein containing both PAZ and PIWI domains. Overexpression of this gene in rice induced upward curling of the leaf blade. The AGO proteins are essential components of RNA-induced silencing complexes (RISCs) and critical in directing the interaction between the miRNA and the target mRNA for cleavage or translational repression.

Erect leaf is the only common phenotype among all BR-related mutants, indicating that is the most sensitive of the BR-related phenotypes (Morinaka *et al.*, 2006). For example, the *BR-deficient dwarf1* (*brd1*) mutant is defective in C-6 oxidase, which catalyzes the C-6 oxidation step in BR biosynthesis (Hong *et al.*, 2002); another BR-deficient mutant, *D2*, was defective in cytochrome CYP90D (Hong *et al.*, 2003). Although the *d2* and *brd1* mutants have an erect-leaf phenotype, other morphological alterations in reproductive organs have also been observed, resulting in decreases in grain yield and pollen fertility. Both are unfavorable traits for crop breeding (Morinaka *et al.*, 2006). BR activates its downstream transcription factors BZR1 and BZR2, which belong to the plant-specific BZR protein family in *Arabidopsis*. OsBZR1 is the closest rice homolog of *Arabidopsis* BZR1 (Bai *et al.*, 2007), its RNAi transgenic plants show erect leaves and no BR response in lamina bending. Recently, a new mutant *OsDwarf4*, which has an erect-leaf phenotype and is BR-deficient, has been associated with enhanced biomass production and grain yield under conditions of dense planting. *OsDwarf4* encodes a cytochrome P450, CYP90B2 and CYP724B1, which are the rate-limiting steps in BR biosynthesis (Sakamoto *et al.*, 2006). The results indicate that genetic modification of specific steps in BR biosynthesis can improve crops, with no negative environmental effects.

Plant architecture and genetic improvement in rice

Ideotype—or desired plant type—breeding and the use of hybrid vigor are two main approaches to improve

crops. In China, super rice breeding combines both approaches to develop new elite varieties and increase grain yield potential. Improved high-yield rice varieties such as Shanyou 63, a widely grown cultivar in China (Figures 3c, e and 4a), have some of the properties of desired plant types, including medium plant height and moderate tillering capacity. Ideotype breeding of rice, also called modification of plant architecture, as in Yuan's (1997) model for rice, includes the following desired morphological traits (Figures 3d and 4b) medium plant height for higher harvest index; moderately compact growth habit and moderate tillering capacity for optimum panicles; top three functional leaves that are more erect, thicker, longer and slight rolled for more efficient use of light energy and photosynthesis; and heavy, droopy heavy panicle for more dry matter accumulation (Yuan, 1997).

The number of panicles per unit area is an important determinant of yield potential. Although some genes that control tiller formation have been cloned, it is very difficult to design a plant with a specified optimal number of tillers in field because tillering capacity is regulated not only by different kinds of genes but by environmental factors and cultivation practices. The conventional breeding method remains the most common way of selecting varieties with moderate tillering capacity that can produce optimal effective tillers for bigger panicle formation. Optimizing the tiller angle (that is, to produce a moderately compact growth habit) of rice cultivars continues to be a target of breeding programs today. Tiller angle determines the density of planting, which affects the total number of effective panicles in the field. Improvement in the tiller angle makes plants more efficient at trapping light for photosynthesis and may also allow plants to avoid some diseases by decreasing humidity. Recently, the QTL gene *TAC*, which controls tiller angle, was characterized and cloned, indicating that it is possible to create a new rice plant type with a moderate tiller angle by modifying expression level of *TAC* in transgenic plants (Yu *et al.*, 2007).

The height of rice plants is another decisive factor in grain yield potential. Zou *et al.* (2003) proposed that plant height and leaf angle are two the most important factors in the breeding of super rice breeding, along with breeding experience. Semi-dwarf varieties are more resistant to wind and rain damage than their taller counterparts and also produce higher grain yields

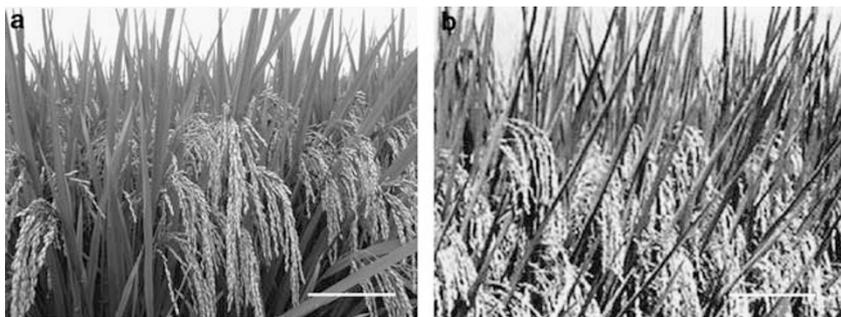


Figure 4 The population comparison of two different high-yielding rice cultivars by plant type. The improved high-yield variety has normal top functional leaves and the super high-yield variety has desired leaf shape and small leaf angle. (a) An elite hybrid variety, Shanyou 63, with improved plant type. (b) A super hybrid rice variety, Lianyoupeijiu, with desired plant type. The panicles are droopy and lower than the top three leaves and the top three functional leaves are erect, longer and slight rolled. Bar, 8.3 cm.

because more resources are allocated to the grain rather than to the vegetative tissues. As described above, GA and BR are two major factors that determine plant height. The complexity of the GA and BR signaling pathways provides numerous possible points for manipulation of plant height and it is likely that different approaches will be required to manipulate the expression of height-controlling genes in the appropriate tissues. For example, controlling expression of GA 2-oxidase gene in specific tissue resulted in semi-dwarf phenotype (Sakamoto *et al.*, 2003), suggesting that genetic modification of the GA signaling pathway could have great potential for creating semi-dwarf plants in rice breeding programs.

Kernel weight is also a key factor in grain yield potential. Light energy utilization and efficient photosynthesis by the top three leaves of rice stem are the primary means of the carbohydrates production that fills grains. Increasing kernel weight by improving the rate of biomass production can enhance grain yield potential at grain-filling stage. Erect leaves have a higher leaf area index (single-side leaf area per unit of land area), which increases the capture of light for photosynthesis and nitrogen use in dense plantings. This in turn improves dry matter accumulation in panicles and increases yield (Sinclair and Sheehy, 1999). Most of the high-yielding varieties, including the super high-yielding hybrid rice, Liangyoupeijiu, have a small leaf angle and erect-leaf canopies (Figures 3f and 4b). Compared with a widely grown cultivar in China such as Shanyou 63, the top three functional leaves of Liangyoupeijiu have more photosynthetic capacity and sustain high-level photosynthesis for longer periods of time, suggesting that the top three functional leaves of these high-yielding varieties have a higher net photosynthetic rate and greater ability for dry matter accumulation. Loss-of-function mutations in *OsDWARF4* cause more modest dwarfing and increase leaf erectness, but do not affect seed size. A small field trial of plants carrying the *Osdwarf4-1* mutant allele using two planting densities and three levels of nitrogen revealed that the *Osdwarf4-1* plants produced 40% more biomass compared with wild-type plants at all nitrogen levels under in a dense planting environment (Sakamoto *et al.*, 2006).

A rolled- or V-shaped leaf is regarded as another important factor in rice yield. These distinctive shapes make leaves stiffer along the longitudinal axis, thus providing additional support and decreasing droopiness. In rice varieties with rolled leaves, some data indicate that the photosynthetic rate, biomass and yield of the top leaves are higher in medium- and high-density populations, suggesting that the advantage of varieties with rolled leaves can be maximized through a reasonable increase in planting density (Shi *et al.*, 2007). In rice, overexpression of the *OsAGO7* gene results in an upward curling of leaves, indicating that it is possible to design plants with rolled leaves by altering expression of the *AGO*-relating genes.

The data outlined above suggest that modifying plant architecture of rice at molecular level to produce an ideotype is a promising approach to increase grain yield. As more mutants with alteration in plant architecture are collected and key regulatory genes are cloned and studied, the genetic network that controls the rice plant

architecture will be uncovered. This will facilitate the improvement of crop varieties through the modification of plant type.

Conclusions

Plant breeders have paid special attention to plant architecture for centuries because of its significance in varieties improvement. Plant architecture is regulated at numerous levels, including genetic determination and hormone signaling pathways. Our knowledge of the underlying molecular basis of plant architecture in rice has been accumulated mainly through the characterization of rice mutants. In recent years, significant progress has been made: a novel hormone signaling pathway has been shown to regulate rice tillering and plant height; and other regulators, including GA and BR, have been identified and their roles in modulating plant height and leaves angle elucidated. Although our present knowledge of plant architecture is still not complete, numerous mutants generated using T-DNA or transposon/retrotransposon tagging approaches will facilitate the identification of the related functional genes associated genetic network that controls the rice plant architecture. On the basis of current knowledge, we are left with the challenge of thinking up new molecular strategies that combined with conventional breeding methods, will enable us to develop the desired type of plant architecture that results in optimal yields.

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