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REVIEW

The genetic and molecular basis of crop height based on a rice model

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Abstract

Main conclusion **This review presents genetic and molecular basis of crop height using a rice crop model. Height is controlled by multiple genes with potential to be manipulated through breeding strategies to improve productivity.**

Height is an important factor affecting crop architecture, apical dominance, biomass, resistance to lodging, tolerance to crowding and mechanical harvesting. The impressive increase in wheat and rice yield during the 'green revolution' benefited from a combination of breeding for high-yielding dwarf varieties together with advances in agricultural mechanization, irrigation and agrochemical/fertilizer use. To maximize yield under irrigation and high fertilizer use, semi-dwarfing is optimal, whereas extreme dwarfing leads to decreased yield. Rice plant height is controlled by genes that lie in a complex regulatory network, mainly involved in the biosynthesis or signal transduction of phytohormones such as gibberellins, brassinosteroids and strigolactones. Additional dwarfing genes have been discovered that are involved in other pathways, some of which are uncharacterized. This review discusses our current understanding of the regulation of plant height using rice as a well-characterized model and highlights some of the most promising research that could lead to the development of new, high-yielding varieties. This knowledge underpins future work towards the genetic improvement of plant height in rice and other crops.

Keywords Plant height · Dwarf gene · Rice · Gibberellins · Brassinosteroids · Strigolactones · Agronomic trait · Breeding

Introduction

Over the past 40 years, the human population has doubled, reaching 7.3 billion people in 2016 and predicted to reach 9.1 billion by 2050. The Food and Agriculture Organisation (FAO) estimates that market demand for food will follow

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at the same pace. Demand for cereals, for both human consumption and animal feed, is projected to reach some 3 billion tonnes by 2050, up from today's demand of ~ 2.1 billion tonnes. To meet this demand requires a 70% increase in food production from the levels seen in 2005/07 (FAO 2009, http://www.fao.org/docrep/012/i0680e/i0680e.pdf).

Significant increases in global food production occurred in the 1960s and 1970s during the 'Green Revolution', where impressive gains in the yields of wheat and rice doubled production in most parts of the world (Hargrove and Cabanilla 1979; Khush 1999). The biggest contributors to this were the breeding of semi-dwarf, high-yielding varieties, in combination with new fertilizer and pesticide technologies. Dwarfing was attributed to the plants' genetic inability to synthesize or respond to certain phytohormones, predominantly gibberellins (GAs). GAs are perturbed in recessive mutants of *semi dwarfing 1* (*sd1*) (Monna et al. 2002; Sasaki et al. 2002; Ashikari et al. 2002) as well as one of two *reduced height 1* (*Rht-B1* and *Rht-D1*) (Peng et al. 1999; Hedden 2003) (Fig. 1a, b). Alleles of *sd1* and *Rht1* have been deployed in breeding of commercial rice and wheat varieties, respectively. Dwarfed rice varieties containing *sd1* alleles offer several advantages over taller varieties, including more efficient use of fertilizers, resistance to lodging, greater tillering and a higher harvest index (Monna et al. 2002). The GA-insensitive *Rht-B1b* and *Rht-D1b* dwarfing mutants in wheat alter plant and canopy height, show reduced crop lodging and greater dry-matter, which results in increase grain number, harvest index and grain yield (Bonnett et al. 2001; Chapman et al. 2007).

However, the benefits of GA-insensitive semi-dwarfs are greatest in favorable environments such as a higher-yielding, irrigated environment (Butler et al. 2005; Chapman et al. 2007). The rising temperatures as a consequence of climate change will have negative impact on GA-insensitive dwarfing mutants (Rebetzke et al. 2012). Moreover, the overuse of limited dwarf genetic materials like *sd1* and *Rht1* runs the risk of losing genetic diversity. There is a need to expand the range of dwarf source material, to identify new genes by functional genomics, and to exploit these genes in practice. Understanding dwarfing has thus become a major focus of research in crop genetics and genomics, which has led to many great advances (Ikeda et al. 2001; Sasaki et al. 2002, 2003; Hong et al. 2003; Ueguchi-Tanaka et al. 2000, 2005; Tanabe et al. 2005; Arite et al. 2007). Apart from the rice *sd1* gene and the wheat *Rht1* gene, other genes contributing to both crop height have been cloned in the GA biosynthesis/signaling pathway (Ashikari et al. 1999; Ueguchi-Tanaka et al. 2000; Sasaki et al. 2002, 2003; Itoh et al. 2004) as well as that of other hormones including brassinosteroids (BRs) (Hong et al. 2003; Tanabe et al. 2005) and strigolactones (SLs) (Lin et al. 2009), indole-3-acetic acid (IAA), abscisic acid (ABA), ethylene (ETH) and Jasmonate (JA). Dwarfing non-hormone pathways have also been described (Arite et al. 2007).

Despite high-yielding mutants, some dwarfing mutants defective in hormone biosynthesis or signaling often display pleiotropic phenotypes that negatively affect productivity via altered tillering, stem physiology and fertility. Such affects include small grains, semi-sterility and malformed panicles

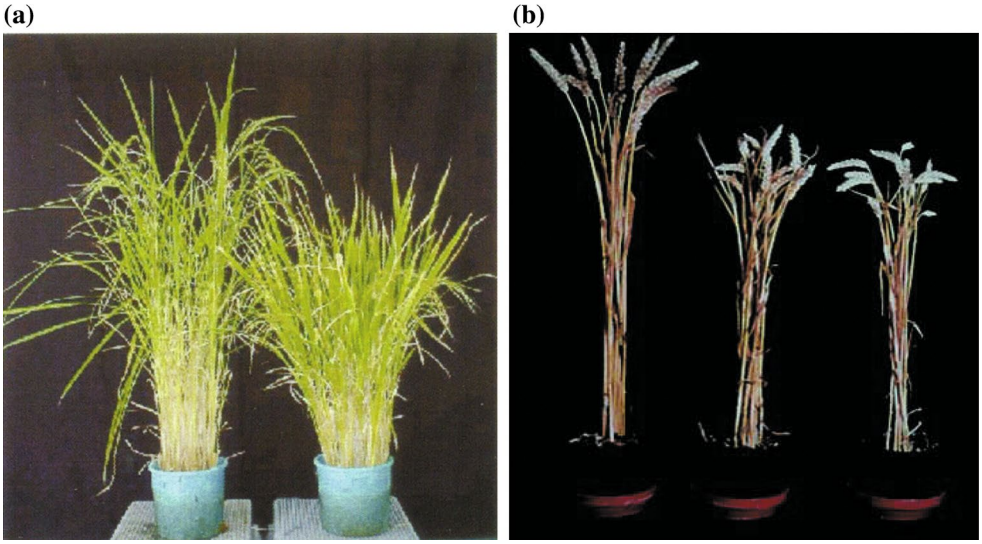

Fig. 1 The phenotypic effect of key dwarfing genes that were utilized during the 'green revolution'. **a** Stature of normal-type (right, Taiwanese indica strain woo-gen) and semi-dwarf type (left, dee-geo-woo-gen, containing a 383-base-pair deletion of *sd-1* which introduces a stop codon and produces a truncated, inactive enzyme) rice. The figure is derived from Hedden (2010). **b** Stature of normal-type (left, cultivar Mercia) and semi-dwarf (centre, *Rht-B1b*; right, *Rht-D1b*) near-isogenic wheat lines. The figure is derived from Peng et al. (1999)

(Butany et al. 1959; Sazuka et al. 2009; Asano et al. 2010). Thus the productivity phenotype cannot be definitively attributed to the dwarfing effect itself. Nonetheless, despite this potential for unwanted alleles, it is important that the search continues for novel semi-dwarf genes.

In this review, we describe how crop height can be manipulated to improve crop yield. We explain the genetic and physiological basis of crop dwarfing, including the molecular mechanisms that regulate rice plant height. Finally, we show an application of rice plant height genes in crop breeding and offer suggestions for future research towards new strategies to control crop.

Relationship between crop height and yield

Plants that are dwarfed have been associated with yield increases and yield stability (Peng et al. 1999). There are different categories of dwarfing, namely semi-dwarf, dwarf and extra-dwarf, which refer to varieties that, respectively, attain 50–100%, equal to or slightly less than 50% and substantially less than 50% of the mature height of a wild-type plant (Futsuhara and Kikuchi 1997). Semi-dwarfing increases grain yield per unit area in a variety of ways by allowing (1) planting at higher densities (Mori et al. 2002; Hong et al. 2005), (2) reducing apical dominance and, therefore, promoting tillering (Alder et al. 2012; Waters et al. 2012; Wei et al. 2013), (3) reducing the final biomass and, therefore, increasing the economic coefficient (or harvest index) (Fischer and Quail 1990; Zhang et al. 2014a) and (4) providing greater resistance to lodging (Hedden and Phillips 2000). Enhanced lodging resistance also facilitates mechanical harvesting (Fig. 2).

Excessive dwarfing is often correlated with poor agronomic traits, such as smaller grains, excessive tillering, narrower or rolled leaves and poor disease resistance (Ueguchi-Tanaka et al. 2000; Tanabe et al. 2005; Arite et al. 2007; Li et al. 2009). On the other hand, when a plant is excessively tall, the stems are too weak to support the weight of the head of high-yielding varieties, and they are susceptible to lodging by wind and rain subsequently suffering from diseases and insect pests. Through a combination of these observations, it is assumed that the relationship between crop height and yield follows a bell curve, peaking when the leaf area index (green leaf area per unit ground surface area) reaches the optimal value (Begonia and Begonia 2007). However, the relationship between crop height and yield is affected by a number of factors, such as environment (Botwright et al. 2005; Chapman et al. 2007; Rebetzke et al. 2012), where the bell curve is swayed one way or another. Indeed, there are still situations where tall isolines may yield the same or better than short isolines (Chapman et al. 2007). In general, however, studies indicate wheat yields are maximised within a height range of 70–100 cm (Richards 1992; Flintham et al. 1997; Botwright et al. 2005).

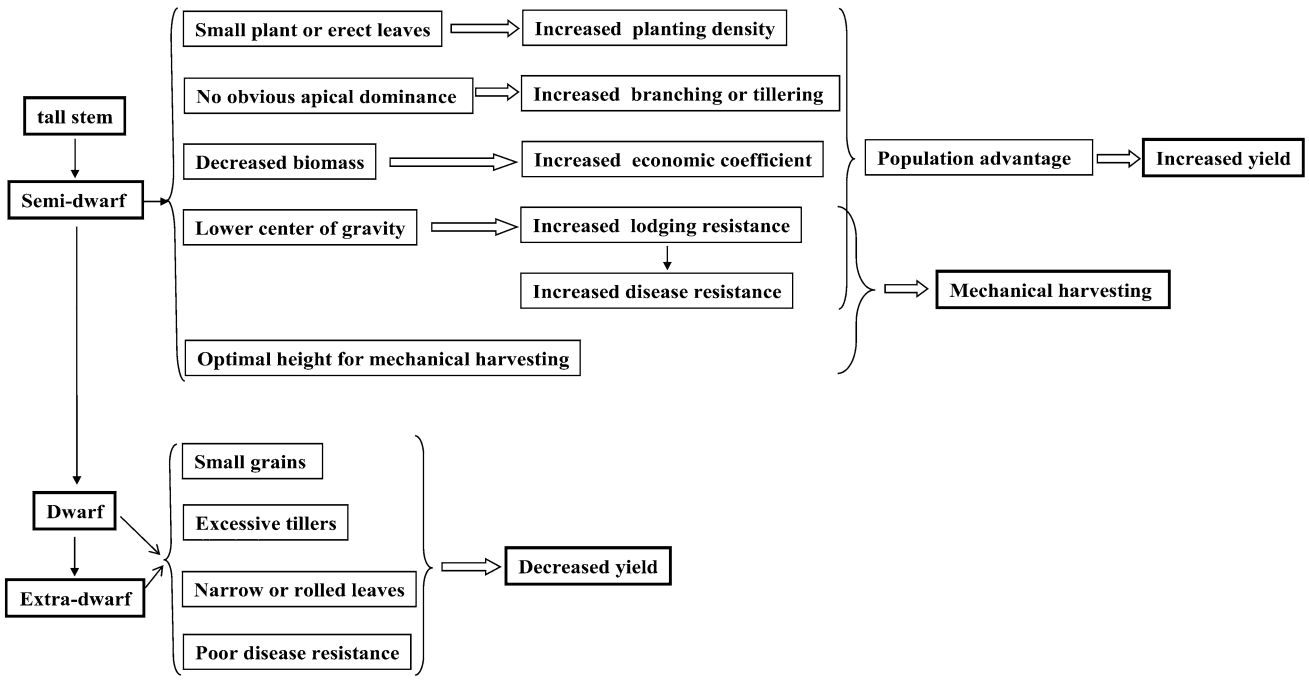

Fig. 2 Flow chart showing how crop height influences yield

Genetic basis of crop height

Rice plant height is mainly controlled by one to three major genes but modulated by minor genes (Butany et al. 1959; Iwata et al. 1977; Saeda and Kitano 1992; Liu et al. 2008). Most natural or artificially induced dwarf mutants of the 'indica-type' varieties are homozygous for the semi-dwarf gene *sd1* and are only rarely controlled by two, three or more genes. A similar situation exists with 'japonica-type' rice varieties (Butany et al. 1959; Iwata et al. 1977; Saeda and Kitano 1992; Liu et al. 2008). The naming of rice dwarf genes has been standardized, where d denotes dwarf and sd, semi-dwarf (Mitsunaga et al. 1994; Iwata et al. 1995). The genes have been numbered according to the chronology of discovery, with 62 *d* and 15 *sd* genes registered (Kinoshita 1995). They can be roughly divided into three categories: (1) the same as the *sd1* locus, (2) sharing a complex locus with *sd1* and (3) not co-located with *sd1* locus (Chang et al. 1984; Murai et al. 1990).

Paradoxically, the study of factors leading to excessive height has contributed to a better understanding of dwarfism. In 1981, the American scholars Rutger and Carnahan reported a mutant rice plant '*76: 4512*', which had an elongated uppermost internode (elongated uppermost internode stock). The gene causing this phenotype, which is not linked to *sd1*, was named *ELONGATED UPPERMOST INTERNODE* (*EUI*) (Rutger and Carnahan 1981). Crossing experiments demonstrated that *EUI* was completely or incompletely dominant over *sd1* in rice.

Maize plant height is divided into three types: tall (more than 2.5 m), moderate (1.8–2.5 m) and dwarf (less than 1.8 m), controlled by single genes or polygenes. At present, a total of 20 dwarfing genes have been found in maize, but only 17 have been mapped. With the exception of *DWARF8* (*D8*), *DWARF9* (*D9*) and *DWARF8* (*D11*), most of these genes are recessive and are characterized as single-gene traits (Emerson et al. 1935; Neuffer et al. 1997; Lawit et al. 2010; Wang et al. 2013a, b).

Wheat plant height is controlled by major genes and modulated by several other modifier genes. In wheat, the major dwarfing genes belong to the *Rht* family, wherein 26 dwarf genes have been identified. Nine of these have been mapped, and five are recessive (Mcintosh 1988). Most research has focused on *Rht1*, *Rht2*, *Rht3*, *Rht8*, *Rht9*, *Rht10*, *Rht12* and *Rht13*, with each having a different effect on yield. Multivarietal comparisons have shown that cultivated semi-dwarf varieties carrying the *Rht1* and *Rht2* genes are better yielding than the taller stem commercial varieties (Miralles and Slafer 1995; Beharav et al. 1998; Botwright et al. 2005; Rebetzke et al. 2011, 2012; Wang et al. 2014).

In barley, several short-statured genotypes have been identified that possess the semi-dwarf genes *uzu* and *sdw1* and have been widely used in breeding programs to reduce lodging and to improve the harvest index (Sears et al. 1981; Foster and Thompson 1987; Li et al. 2015).

Rapeseed dwarf mutants are also divided into two types. Mutants of one type are controlled by dominant or recessive genes and mutants of the other type are controlled by polygenes. More than ten dwarf or semi-dwarf mutants have been reported in rapeseed, but only one dwarfing gene has been successfully cloned (Foisset et al. 1995; Muangprom and Osborn 2004).

Mechanisms controlling plant height in rice

The mechanisms and genes controlling plant height have been more thoroughly investigated in rice than in any other crop. Some of the mapped genes in other species are homologous to rice genes controlling a similar metabolic pathway; however, the mechanisms controlling plant height of other crops are limited by relative lack of genomic information and research tools. Therefore, this section will focus on examples from rice as a model crop, for broad extrapolation to other species.

The various pathways controlling height are shown in Supplementary Table 1. The phytohormones influencing crop height are GAs, BRs, SLs, IAA, ABA, ETH (Ashikari et al. 1999; Ueguchi-Tanaka et al. 2000; Sasaki et al. 2002, 2003; Hong et al. 2003; Itoh et al. 2004; Tanabe et al. 2005; Lin et al. 2009). Dwarf mutants influenced by phytohormones can be divided into two types according to their responsiveness to exogenous hormones. In loss-of-function dwarf mutants, the hormone synthesis pathway is blocked or inhibited, and normal plant growth can be restored by application of the hormone that is missing. In insensitive dwarf mutants, the endogenous hormone levels are similar to, or even higher than in the wild-type plant, but there are blockages in the hormone signal transduction pathways and normal plant growth cannot be restored by applications of the hormone (Supplementary Table 1). Dwarf mutants influenced by non-hormone factors are mainly involved in several pathways including cell wall development, cytosolic glutamine synthetic pathway, RNA editing, cell division, ubiquitin–proteasome pathway and fatty acid metabolism. In addition, there are genes controlling plant height in rice from as yet uncharacterised pathways.

Genes controlling rice plant height that relate to phytohormone pathways

GA-related pathways

GAs comprise one of the major hormone groups in higher plants and consist of tetracyclic diterpenoid phytohormones, with 136 different compounds currently known (Hedden and

Thomas 2012). The GAs play a role in many aspects of plant growth and development, such as stem or internode elongation, flower and fruit development and seed germination (Ross et al. 1997; Ayano et al. 2015). GA-deficient and GA-insensitive mutants are usually much shorter than wild-type plants.

Genes involved in GA biosynthesis Bioactive GAs, such as GA_1 and GA_4, are synthesized from *trans*-geranylgeranyl diphosphate (GGDP) through the action of *ent*-copaly diphosphate synthases (CPS) and *ent*-kaurene synthase (KS) in the plastids; by *ent*-kaurene oxidase (KO), *ent*-kaurenoic acid oxidase (KAO) and GA 13-oxidase (GA13ox) on the endoplasmic reticulum membrane and through two parallel pathways in the cytoplasm involving GA 20-oxidase (GA20ox) and GA-3β-hydroxylase/GA 3-oxidase (GA3ox) (Hedden and Kamiya 1997; Hedden and Phillips 2000) (Fig. 3).

In recent years, dwarf genes involved in the GA biosynthesis and catabolism pathways (*CPS*, *KS*, *KO*, *KAO*, *GA20ox*, *GA3ox*) have been characterized from various plant species (Hedden and Phillips 2000; Luo et al. 2006; Zhu et al. 2006) (Fig. 3; Table 1). The semi-dwarf phenotype of the *sd1* mutant (Fig. 1a) is the result of a deficiency of active GAs in the elongating stem resulting from a mutation in the *OsGA20ox2* gene (Ashikari et al. 2002; Monna et al. 2002; Sasaki et al. 2002; Spielmeyer et al. 2002). This gene has been extensively used in rice breeding due to its high heritability and minimal impact on other agronomic traits. Most semi-dwarf genes in 'indica-type' varieties are *sd1* alleles. The *d18* and *d35* mutants have defective *OsGA3ox2* and *OsKO2* genes, respectively (Ogawa et al. 1996; Itoh et al. 2001, 2004; Sakamoto et al. 2003), which affect the GA

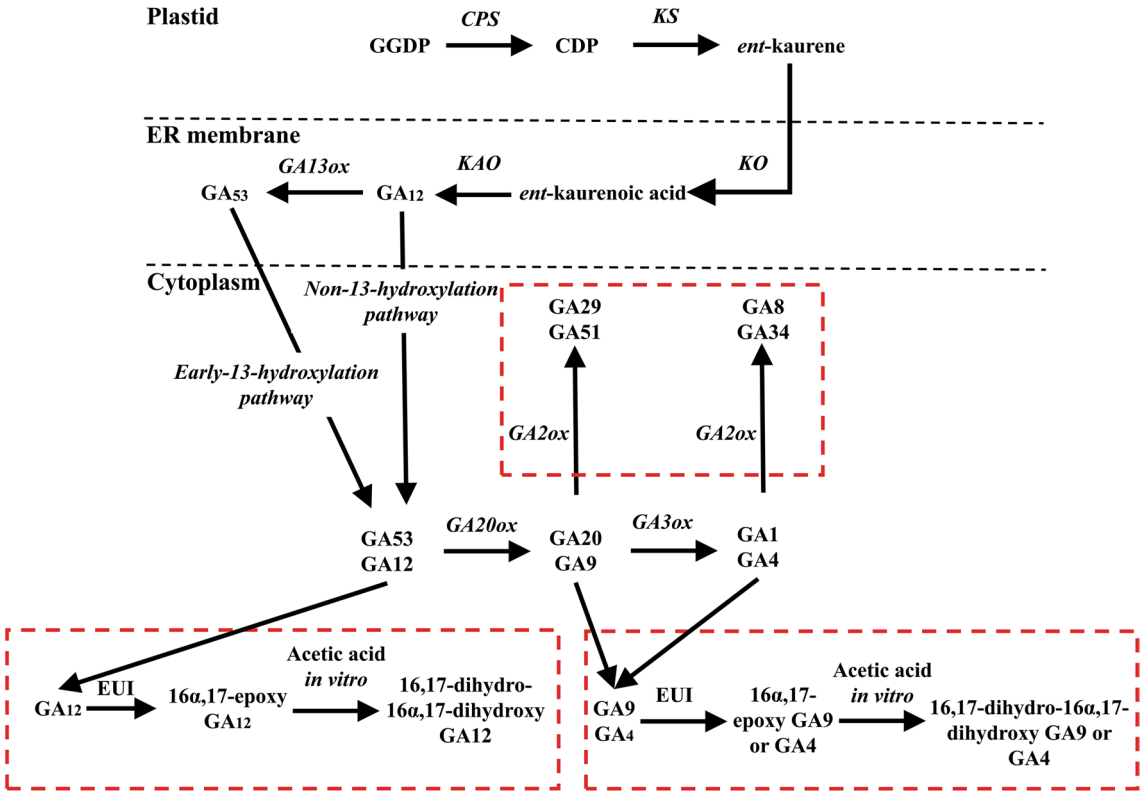

Fig. 3 Principal pathways of gibberellin (GA) biosynthesis and catabolism (see boxes with red dashed lines) in crop species. GA biosynthesis: *trans*-geranylgeranyl diphosphate (GGDP) is converted to the tetracyclic hydrocarbon *ent*-kaurene via *ent*-copalyl diphosphate (CDP) by two kinds of diterpene cyclases in plastids, CDP synthase (CPS) and *ent*-kaurene synthase (KS). ent-Kaurene is then modified by sequential oxidations to produce GA_{12} via ent-kaurenoic acid. These steps are catalyzed by two membrane-associated cytochrome P450 monooxygenases, *ent*-kaurene oxidase (KO) and *ent*-kaurenoic acid oxidase (KAO). The final stage of bioactive GA synthesis, from GA_{53}/GA_{12} to GA_1/GA_4, is catalyzed through two parallel pathways (early-13-hydroxylation and non-13-hydroxylation pathways) by two soluble 2-oxoglutarate-dependent dioxygenases (2ODDs) in the cytosol (GA 20-oxidase (GA20ox) and GA 3-oxidase (GA3ox)) (Sakamoto et al. 2004). GA catabolism: The bioactive GA_1/GA_4 and their immediate precursors GA_{20}/GA_9 are inactivated by a third 2ODD, GA 2-oxidase (GA2ox) (Thomas et al. 1999; Hedden and Phillips 2000; Olszewski et al. 2002; Schomburg et al. 2003; Lee and Zeevaart 2005); GA_{12}, GA_9, and GA_4 are converted to 16α,17-epoxy derivatives by ELONGATED UPPERMOST INTERNODE (EUI). The epoxides are chemically converted to 16,17-dihydro-16α,17-dihydroxy GAs when the products are purified in the presence of 1% acetic acid (Zhu et al. 2006)

Table 1 Plant height genes involved in gibberellic acid (GA) biosynthesis, catabolism, homeostasis and signal transduction in rice

Pathway	Enzyme name	Gene product	Gene name	Mutant/transgenic name	Chrom. location	References
GA biosynthesis	CPS	*Ent*-copaly diphosphate synthase	*OsCPS1*	*oscps*	2	Sakamoto et al. (2004), Tomonobu et al. (2009)
	KS	*Ent*-kaurene synthase	*OsKS1*	*Osks*	4	Sakamoto et al. (2004), Marcia et al. (2005)
	KO	*Ent*-kaurene oxidase	*OsKO2*	*d35*	6	Ogawa et al. (1996), Itoh et al. (2004)
	KAO	*Ent*-kaurenoic acid oxidase	*OsKAO*	*oskao*	6	Sakamoto et al. (2004)
	GA20ox	GA 20-oxidase	*OsGA20ox2*	*sd1*	1	Ashikari et al. (2002), Monna et al. (2002), Sasaki et al. (2002)
	GA3ox	GA 3-oxidase	*OsGA3ox2*	*d18*	1	Itoh et al. (2001), Sakamoto et al. (2003)
	GA2ox	GA2-oxidase	*OsGA2ox6*[a]	*35S::OsGA2ox6*	4	Lo et al. (2008), Huang et al. (2010)
	EUI	GA 16α,17-epoxidase	*OsEUI*[a]	*eui*[b]	5	Luo et al. (2006), Zhu et al. (2006)
	YAB	YABBY	*OsYAB1*[a]	*35S::OsYAB1*	7	Dai et al. (2007), Toriba et al. (2007)
	DOG	A20/AN1 zinc-finger protein	*OsDOG*[a]	*Ubi::OsDOG*	8	Liu et al. (2011)
GA signal	–	–	*OsGID1*	*gid1*	5	Ueguchi-Tanaka et al. (2005), Hirano et al. (2010)
	Gα	α subunit of the heterotrimeric G protein	*OsD1/OsRGA1*	*d1*	5	Ashikari et al. (1999), Ueguchi-Tanaka et al. (2000)
GA signal	SPY	O-linked *N*-acetylglucosamine transferase	*OsSPY*[a]	*OsSPY RNAi*[b]	8	Shimada et al. (2006)
	SLR1	DELLA protein	*OsGAI*[a]	*slr1*[b]	3	Ogawa et al. (2000), Ikeda et al. (2001), Asano et al. (2009), Hirano et al. (2012)
	CIGR	Chitin-inducible gibberellin-responsive protein	*OsCIGR*[a]	*ph1*[b]	1	Kovi et al. (2011)
	GID	F-box subunit of SCF E3 complex	*OsGID2*	*gid2*	2	Sasaki et al. (2003), Gomi et al. (2004)
	–	–	*OsDNL1*	*dnl1*	12	Wei et al. (2013)

[a]It is a negative regulated gene in the pathway

[b]The phenotype of mutant or transgenic plant is tall stem

biosynthesis pathway. Sakamoto et al. (2004) performed a large-scale screening of rice mutants, and identified nine novel dwarf mutant lines with recessive alleles, including two alleles of *cps*, three alleles of *ks*, one allele of *ko2* and three alleles of *kao*. These mutants are characterized as being GA-deficient as applications of active GA can restore the wild-type phenotypes (Table 1).

Rice plant height can also be altered by modifying the GA catabolism pathways. The aforementioned genes *GA20ox* and *GA3ox* function in GA biosynthesis and are involved in feedback regulation, while *GA 2-oxidase* (*GA2ox*) functions in GA catabolism and is involved in feedforward regulation by bioactive GAs (Hedden and Phillips 2000; Olszewski et al. 2002) (Fig. 3). Bioactive GA_1 and GA_4 and their precursors, GA_{20} and GA_9, can be inactivated by GA2ox via 2β hydroxylation (Thomas et al. 1999; Hedden and Phillips 2000; Olszewski et al. 2002; Schomburg et al. 2003; Lee and Zeevaart 2005) and *GA2ox* mutants do not show a typical dwarf phenotype (Sakamoto et al. 2004). Huang et al. (2010) isolated a CaMV 35S enhancer-labeled mutant in rice, which showed dominant dwarfing with enhanced expression of the *Os2ox6* allele gene: endogenous GA activity decreased and

applications of GA could recover the phenotype. Moreover, ectopic expression of *OsGA2ox1* allele gene driven by the promoter of the GA biosynthesis gene *GA3ox2*, led to a semi-dwarf phenotype, suggesting its potential for improving yield in rice (Sakamoto et al. 2003; Table 1).

Zhu et al. (2006) demonstrated another GA deactivation mechanism, involving the rice *EUI* gene (Luo et al. 2006), which encodes a P450 monooxygenase that catalyzes 16α,17-epoxidation of non-13-hydroxylated GAs to generate bio-inactive 16α,17-[OH]2-GAs (Fig. 3). *eui* is a long stem mutant of rice and the plant accumulates extremely high levels of GA_1 and GA_4 (Zhu et al. 2006). The constitutive overexpression of this gene in transgenic plants significantly reduces the GA levels, resulting in severe dwarf phenotypes (Zhu et al. 2006). Male sterile cultivars of rice are commonly defective in elongation of the uppermost internode due to inadequate GA production by the empty anthers (Li and Yuan 2000), and the *EUI* gene is a useful breeding target as mutations to this gene improve the heading performance of rice male sterile cultivars in hybrid rice production (Shen and He 1989; He and Shen 1991; Yang et al. 2002; Table 1).

GA homeostasis is maintained via feedback and feedforward regulation of GA levels by major target genes like *GA20ox*, *GA3ox* and *GA2ox* (Yamaguchi 2008), but how regulation is achieved is not fully understood. The gene products of *Oryza sativa YABBY 1* (*OsYAB1*) directly bind to the promoter of *GA3ox2* gene and suppress its expression and, therefore, act negatively in GA feedback regulation. Overexpression of *OsYAB1* in transgenic rice results in a semi-dwarf phenotype that can be fully rescued by applications of GA (Dai et al. 2007). Liu et al. (2011) reported that *Oryza sativa DWARF RICE WITH OVEREXPRESSION OF GIBBERELLIN-INDUCED GENE* (*OsDOG*) was induced by GA_3 and repressed by a GA-synthesis inhibitor. Transgenic lines with constitutively expressed *OsDOG* have decreased levels of GA_1 and retarded cell elongation, leading to dwarfing. The decrease of GA_1 in the *OsDOG* overexpression lines is due to reduced expression of *GA3ox2* and increased expression of *GA2ox1* and *GA2ox3*. *OsDOG* is suggested to have a novel function in feedback regulation of GA homeostasis by binding DNA or protein, through A20 and/or AN1 zinc fingers that interact with GA metabolism genes (Table 1).

Genes involved in GA signaling Most of the components involved in the GA signaling pathway have been identified in rice through genetic screens during the past decade. The most important components include the GA receptor GIBBERELLIN INSENSITIVE DWARF 1 (GID1), the DELLA growth inhibitors (e.g., SLENDER 1 (SLR1)) and the F-box proteins GIBBERELLIN INSENSITIVE DWARF2 (GID2) (Achard and Genschik 2009). The GA-GID1-DELLA pathway, which is the basic GA signal transduction pathway, has been established (Ikeda et al. 2001; Sasaki et al. 2003; Ueguchi-Tanaka et al. 2005) (Fig. 4a). GID2 is the F-box protein subunit of the SKP-CULLIN-F-BOX (SCF) E3 ubiquitin-ligase complexes (Sasaki et al. 2003). In the presence of SCF^{GID2}, GA triggers the degradation of DELLA proteins through the SCF-mediated 26S proteasome system (Ikeda et al. 2001) (Fig. 4a). As a negative regulator of GA signal transduction, SLR1 interacts with GID1 and GID2, mediating GA signaling to regulate rice growth and development (Sasaki et al. 2003; Ueguchi-Tanaka et al. 2005). The current GA action model proposes that the DELLA proteins inhibit plant growth, while the GA signal promotes plant growth by overcoming this inhibition (Harberd 2003; Achard and Genschik 2009). In other words, GA is an 'inhibitor of an inhibitor' (Harberd et al. 2009).

GA-response mutants include those with alterations in both GA perception and GA signal transduction. GA perception (i.e. receptor) mutants are GA-insensitive dwarfs, which display a similar dwarf phenotype to GA-deficient mutants, except that they fail to respond to exogenous GA (Ueguchi-Tanaka et al. 2000, 2001, 2005; Sasaki et al. 2003; Harberd et al. 2009; Hirano et al. 2010). While most plants with constitutive GA responses are DELLA loss-of-function mutants, which display a similar phenotype to plants treated with excess GA, like taller stems, paler green leaves and lower fertility, irrespective of bioactive GA levels (Ogawa et al. 2000; Ikeda et al. 2001; Hirano et al. 2012).

The rice mutant *dwarf 1* (*d1*) was the first to be found that was insensitive to applications of GAs; the levels of endogenous GA in the *d1* mutant were significantly higher than in the wild-type plant. The *d1* mutant is defective in the rice heterotrimeric G PROTEIN ALPHA 1 (RGA1 or Gα protein; Ashikari et al. 1999).

Apart from *d1*, the most reported GA signaling pathway mutants associated with dwarfing include the high stem mutant *slr1* (Ikeda et al. 2001), the dwarf mutant *gid1* (Ueguchi-Tanaka et al. 2005) and the dwarf mutant *gid2* (Gomi et al. 2004). *SLR1* maps to the *Oryza Sativa GIBBERELLIN INSENSITIVE* (*OsGAI*) locus in rice (Ogawa et al. 2000), encodes a protein containing a DELLA domain, and has high amino acid similarity to the wheat 'green revolution' genes *Rht-B1b* and *Rht-D1b*, and *Rht-D1a* and the maize 'green revolution' gene *D8*. *slr1* mutant seedlings are two times taller than the wild-type and are not sensitive to GA synthesis inhibitors (Ikeda et al. 2001). Meanwhile, an *slr1* gain-of-function mutant, in which degradation of the SLR1 protein occurs later than in the wild-type, may yield new genetic sources for dwarf breeding (Asano et al. 2009). Analyses of the *gid1* mutant have shown that *GID1* encodes a soluble GA receptor, which has a high affinity to bioactive GAs. By binding to bioactive GAs, GID1 gains the ability to interact with SLR1, forming a GA–GID1–SLR1 complex and thereby inhibits SLR1 or activates ubiquitin degradation

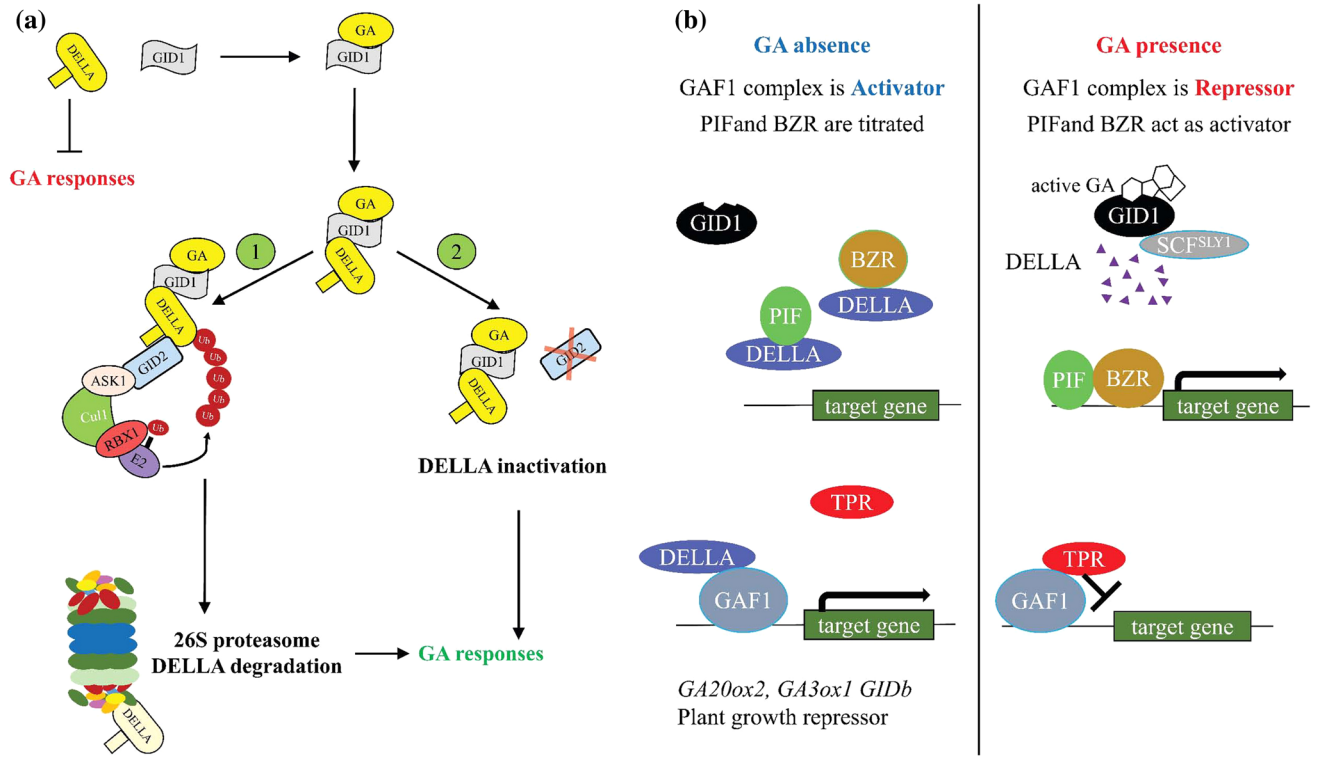

Fig. 4 The model of GA signaling pathway and coactivator and corepressor model for GA signaling in rice and *Arabidopsis*. **a** The model of GA signaling pathway in rice. GA is perceived by the GA receptor GIBBERELLIN INSENSITIVE DWARF 1 (GID1), and the binding of bioactive GA to GID1 enables DELLA, a repressor of GA signaling, to interact with GID1, eventually forming a GA–GID1–DELLA complex. The GIBBERELLIN INSENSITIVE DWARF 2 (GID2) is the F-box protein subunit of the SKP-CULLIN-F-BOX (SCF) E3 complex (Sasaki et al. 2003), The formation of the GA–GID1–DELLA complex promotes interaction between DELLA and the E3 ubiquitin ligase SCF^{GID2}, leading to polyubiquitylation and then degradation of DELLA through the SCF-mediated 26S proteasome system (Ikeda et al. 2001). In the absence of bioactive GAs, DELLAs repress GA responses. In the presence of bioactive GAs, the receptor GID1 is bound by GA, thus promoting its interaction with a DELLA protein. GA represses DELLA activity in two ways: in the absence of SCF^{GID2} activity, the GA-GID1 complex that is bound to DELLAs suppresses their transcriptional activity, whereas the presence of SCF^{GID2} stimulates the degradation of DELLAs (Davière and Achard 2013). The degradation or eventual inactivation of DELLAs relieves DELLA mediated repression of GA responses (Achard and Genschik 2009). **b** A coactivator and corepressor model for GA signaling in *Arabidopsis*. Under GA deficient conditions, DELLAs are stable and localized in nuclei. DELLAs titrate PHYTOCHROME INTERCTING FACTORS (PIFs) and BRASSINAZOLE RESISTANT (BZR) transcription factors by inhibiting DNA binding activity, while DELLAs interact with GAI-ASSOCIATED FACTOR 1 (GAF1) and exhibit high transcriptional activity with GAF1. In the presence of GA, DELLAs are degraded via the 26S proteasome pathway. On the one hand, PIF and BZR activate target genes such as PACLOBUTRAZOL RESISTANCE (PRE) and EXPANSIN. On the other hand, the GAF1 TOPLESS RELATED (TPR) complex exhibits transcriptional repression activity. GA-induced functional conversion of GAF1 complex in plants depends on the degradation of coactivator DELLAs (Fukazawa et al. 2014)

of SLR1 through the SCF^{GID2} complex pathway (Ueguchi-Tanaka et al. 2005). Analysis of the *gid2* mutant has shown that GID2 is an F-box subunit of the SCF E3 complex and that the SCF^{GID2} complex binds with phosphorylated SLR1, inducing ubiquitin-mediated degradation of SLR1 and transduction of the GA signals. In the *gid2* mutant, SLR1 cannot be degraded and GA signaling is inhibited, resulting in a severely dwarfed and sterile phenotype (Sasaki et al. 2003; Gomi et al. 2004; Table 1).

Recently Fukazawa et al. (2015) identified an INDETERMINATE DOMAIN 1 (IDD1) family transcription factor in *Arabidopsis* called GAI-ASSOCIATED FACTOR 1 (GAF1), which can interact with DELLA and TOPLESS RELATED (TPR) in nuclei. DELLAs and TPR act, respectively, as a coactivator and a corepressor of GAF1. GAs convert the GAF1 complex from transcriptional activator to repressor via degradation of DELLAs (Fukazawa et al. 2014, 2015). While this process is well studied in *Arabidopsis* rather than in rice (Fig. 4b).

There are three other genes, including *CHITIN-INDUCIBLE GIBBERELLIN-RESPONSIVE PROTEIN* (*CIGR*), *SPINDLY* (*SPY*) and *DWARF AND NARROW-LEAF 1* (*DNL1*), involved in GA signaling with unclear modes of action: *ph1*, a major QTL on chromosome 1, increases rice plant height and brings forward flowering. Genome annotation suggests that a gene encoding CIGR is likely to be

responsible for the *ph1* phenotype, which mapped with a high degree of accuracy to a region close to *sd1* (Kovi et al. 2011). Within the GAI, RGA, SCR (GRAS) protein super family, which is a plant-specific transcription factor family, *OsCIGR* belongs to the PAT1 branch, while *OsGAI* belongs to the related 'DELLA' branch (Bolle 2004). *OsCIGR* is involved in GA signal transduction but its specific mode of action is unknown. In all of the examined tissues of taller plants, *CIGR* was more highly expressed than in shorter plants, especially in the young leaf sheath containing the elongating cells, indicating an important role of this gene in regulating rice plant height (Kovi et al. 2011).

The second gene, *SPY*, encodes an *O*-fucosyltransferase, which is believed to be a negative regulator of the pathway. In *Arabidopsis*, *O*-fucosylation activates DELLA by promoting its interaction with key regulators in BR- and light-signaling pathways, including BRASSINAZOLE RESISTANT 1 (BZR1), PHYTOCHROME INTERCTING FACTORS 3 (PIF3) and PIF4 (Zentella et al. 2017). In the *OsSPY* antisense or RNAi transgenic rice plants, the increased elongation of lower internodes is correlated with decreased expression levels of *OsSPY*. The suppression of *OsSPY* in the GA-insensitive mutant *gid2* causes increased phosphorylation of the rice DELLA protein SLR1, but does not change concentrations of SLR1. This indicates that the function of *OsSPY* in GA signaling is probably suppressing the function of SLR1 instead of changing the amount or stability of SLR1. In addition, *OsSPY* may play roles both in GA signaling and in the BR pathway (Shimada et al. 2006).

To identify the third gene involved in GA signaling, *OsDNL1*, Wei et al. (2013) examined a dwarf and narrow-leaf mutant *dnl1*, which has a thinner culm, a smaller number of cells in the vertical axis of the internode and more tillers than the wild-type but also a smaller yield. Genetic analyses have shown that this phenotype is due to a single recessive gene, *OsDNL1*, which is located on chromosome 12. *dnl1* is a GA-insensitive dwarf mutant, but its role has yet to be elucidated (Wei et al. 2013; Table 1).

BR-related pathways

BRs are a very important family of plant-specific steroids, which are structurally related to insect and animal steroids. Brassinolide (BL), first isolated and purified from the pollen grains of *Brassica napus*, is the most biologically active of the naturally occurring forms of BR (Grove et al. 1979). More than 50 BL analogues have now been identified (Fujioka and Sakurai 1997). BRs have wide-ranging biological activities and play critical roles in plant development (height, leaf erectness, panicle morphology and seed size) and they are known as a new class of phytohormones (Vriet et al. 2012). Knowledge about BRs has primarily come from studies of BR-deficient and BR-insensitive mutants (Fujioka and Yokota 2003). These mutants typically have dark green, erect leaves and shortened leaf sheaths. Multiple lines of evidence indicate that genetic manipulation of BR biosynthesis or its signaling pathway could significantly improve yield (Choe et al. 2001; Sakamoto et al. 2006; Li et al. 2007; Wu et al. 2008). The BR biosynthesis and signal transduction pathway is much better understood in *Arabidopsis* than in rice (Wang et al. 2012).

Genes involved in BR biosynthesis The various BRs are likely derived from a range of common plant sterols that have an appropriate side chain structure, like campesterol, sitosterol, isofucosterol, 24-methylenecholesterol and 24-epicampesterol. However, campesterol is the only compound that has definitively been shown to be a BL progenitor (Yokota 1997). The biosynthesis pathway for BL can be divided into general sterol synthesis, from cycloartenol to campesterol (Clouse 2002), and the BR-specific pathway from campesterol to BL (Clouse 2002; Zhang et al. 2014a) (Fig. 5). To date, almost all of the key enzymes involved in BR biosynthesis have been characterized in both Arabidopsis and rice.

In rice, one mutant with a defective sterol synthesis pathway and five mutants with defective BR-specific pathways have now been identified (Table 2). *BR-DEFICIENT DWARF 2* (*BRD2*) is homologous to *Arabidopsis DIMINUTO/DWARF 1* (*DIM/DWF1*) and encodes a C-24 reductase that is involved in synthesis of campesterol. The mutant of this gene, *brd2*, produces a semi-dwarf phenotype (Hong et al. 2005). The five genes *DWARF 11* (*D11*), *DWARF4*, *EBISU DWARF* (*D2*), *CONSTITUTIVE PHOTOMORPHOGENESIS AND DWARFISM 1* (*CPD1*), *CPD2*, and *BR-DEFICIENT DWARF 1* (*BRD1*) encode cytochrome P450 family enzymes that are involved in several steps of the BR-specific pathway (Mori et al. 2002; Hong et al. 2002, 2003; Tanabe et al. 2005). With the exception of *OsCPD1* and *OsCPD2*, mutations of these genes cause typical BR knockdown phenotypes, such as dwarfing, erect leaves, shortened internodes and small seeds; the wild-type phenotype can be rescued by applications of bioactive BR compounds (Mori et al. 2002; Hong et al. 2002, 2003, 2005; Tanabe et al. 2005). CYTOCHROME P450 90B2 (CYP90B2)/OsDWARF4 and CYP724B1/D11 are functionally redundant in C-22 hydroxylation (Sakamoto et al. 2006). The loss-of-function mutant *osdwarf4-1* shows a weak BR-deficient phenotype with a slightly dwarfed stature and erect leaves and enhanced grain yields when planted at high densities (Sakamoto et al. 2006). The loss-of-function *d11* mutant has a semi-dwarf and short-grained phenotype (Tanabe et al. 2005). D2/CYP90D2 catalyzes the conversion of 6-deoxoteasterone to 3-dehydro-6-deoxoteasterone, as well as teasterone to 3-dehydroteasterone (Hong et al. 2003). The loss of function *d2* mutant also has a weak BR-deficient phenotype

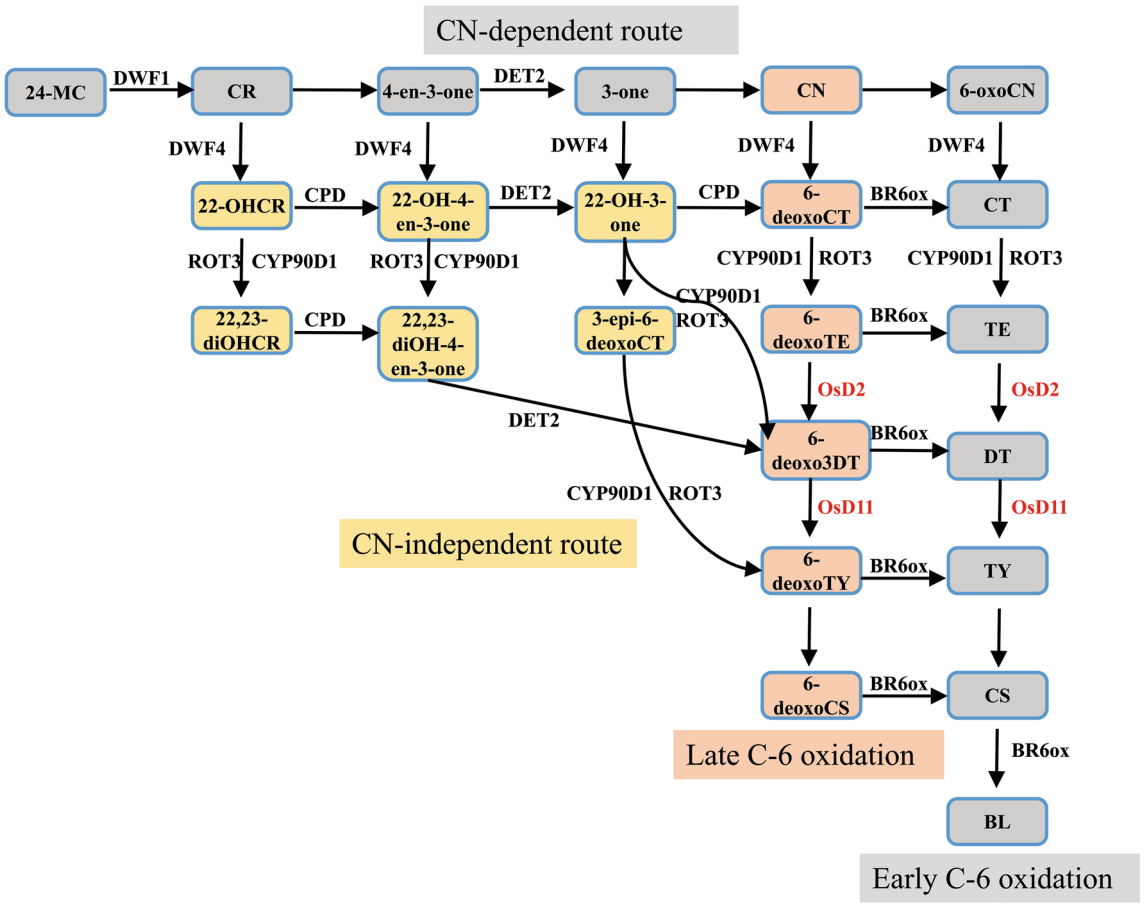

Fig. 5 Brassinosteroid (BR)-specific biosynthesis pathway from campesterol to brassinolide and the enzymes involved in each reaction. The pathway shows most of the enzymes from *Arabidopsis* at the steps indicated, and those in red are enzymes identified only in rice (Hong et al. 2005; Kwon et al. 2005; Tanabe et al. 2005; Vriet et al. 2013). The plant sterol campesterol is converted to brassinolide via castasterone, teasterone, dehydroteasterone, typhasterol and castasteronel. Furthermore, C-6 oxidation could occur before (early C-6 oxidation pathway, the pathway on the left) or after (late C-6 oxidation pathway, the pathway on the right) hydroxylation of the side chain. BR-6-oxidase has been shown to convert 6-deoxo compounds such as 6-deoxocastasterone or 6-deoxotyphasterol to the corresponding 6-oxo compounds in *Arabidopsis* (Zhang et al. 2014a). *CR* campesterol, *CN* campestanol, *CT* cathasterone, *TE* teasterone, *DT* dehydroteasterone, *TY* typhasterol, *CS* castasteronel, *BL* brassinolide

(Hong et al. 2003; Sakamoto et al. 2006). *CYP90A3/OsCPD1* and *CYP90A4/OsCPD2* encode C-3 oxidases, previously suggested to act as BR C-23 hydroxylases (Ohnishi et al. 2006, 2012). *oscpd1*-1, a null mutant of *CYP90A3/OsCPD1*, failed to deliver a BR-deficient phenotype, implying that OsCPD1 and OsCPD2 are functionally redundant and each is capable of catalyzing BR biosynthesis at the required rate for normal growth (Sakamoto and Matsuoka 2006). The *brd1* mutant of rice, which has a defective *BR6 OXIDASE* (*OsBR6OX*) gene, has short leaf sheaths, few tillers and is sterile. The BR6 oxidases in tomato and *Arabidopsis* catalyze multiple C-6 oxidations in BR biosynthesis (Shimada et al. 2001) (Table 2).

Genes involved in BR signaling The signal pathway for BRs is best understood in *Arabidopsis* (Wang et al. 2012). In rice, a few components of the BR signal pathway have been characterized by forward or reverse genetics (Fig. 6). Some of them, such as *Oryza sativa BRASSINOSTEROID INSENSITIVE 1* (*OsBRI1*), *Oryza sativa BRI1 ASSOCIATED KINASE 1* (*OsBAK1*), *Oryza sativa GLYCOGEN SYNTHASE KINASE3 LIKE GENE 1* (*OsGSK1*) and *OsBZR1*, are functional orthologs of known *Arabidopsis* genes. However, orthologs of *PHOSPHATASE 2A* (*PP2A*), *BR SIGNALING KINASES* (*BSKs*) and *BRI1 SUPPRESSOR 1* (*BSU1*), which are also BR signaling genes in *Arabidopsis*, have yet to be identified in rice. Conversely, *Oryza sativa TILLER ANGLE INCREASED CONTROLLER* (*OsLIC*), *Oryza sativa DWARF AND LOW TILLERING* (*OsDLT*) and *Oryza sativa TAIHU DWARF 1* (*OsTUD1*) are BR signaling genes in rice but there no orthologs in *Arabidopsis*, indicating that some BR functions are specific to rice (Fig. 6).

Table 2 Dwarf genes involved in brassinosteroid (BR) biosynthesis and signal transduction in rice

Pathway	Enzyme name	Gene product	Gene name	Mutant/transgenic name	Chrom. location	References
BR biosynthesis	DIM	C-24 reductase	*OsBRD2*	*brd2*	10	Hong et al. (2005)
	CYP724B1	C-22α hydroxylase	*OsDWARF4L1/OsD11/OsCPB1*	*dwarf4l1/d11/cpb1*	4	Tanabe et al. (2005), Wu et al. (2016)
	CYP90B2	C-22α hydroxylase	*OsDWARF4*	*osdwarf4-1*	3	Sakamoto et al. (2006)
	CYP90D2	C-3 oxidase	*OsD2*	*d2/csdd1*	1	Hong et al. (2003), Li et al. (2013)
	CYP90A3	C-3 oxidase	*OsCPD1*	*oscpd1-1*	11	Sakamoto and Matsuoka (2006)
	CYP90A4	C-3 oxidase	*OsCPD2*	/	12	Sakamoto and Matsuoka (2006)
	CYP85A1	BR C6-oxidase	*OsBR6OX/OsBRD1*	*brd1*	3	Mori et al. (2002)
BR signal	BRI1	BR receptor kinase	*OsBRI1*	*d61*	1	Yamamuro et al. (2000)
	BAK1	BRI1-associated receptor kinase 1	*OsBAK1*	*35S::OsBAK1*[b]	8	Wang et al. (2007), Li et al. (2009)
	GSK1/2	Glycogen synthase kinase 1	*OsGSK1*[a]*/OsGSK2*[a]*/OsBIN2*[a]	*35S::OsGSK1/2*	1	Koh et al. (2007), Tong and Chu (2012)
	BZR1	Transcription factors	*OsBZR1*	*OsBZR1 RNAi*	7	Bai et al. (2007)
	LIC	CCCH-type zinc finger protein	*OsLIC*[a]	*35S::OsLIC*	6	Wang et al. (2008), Zhang et al. (2012)
	DLT	Plant-specific GRAS family protein	*OsDLT*	*dlt*	6	Tong et al. (2009)
	ILI1	HLH protein	*OsILI1*	*35S::OsILI1*	4	Zhang et al. (2009)
	IBH1	HLH protein	*OsIBH1*[a]	*35S:OsIBH1*	4	Zhang et al. (2009)
	Gα	α subunit of heterotrimeric G-proteins	*OsD1/OsRGA1*	*T65d1*	5	Oki et al. (2009)
	TUD1	U-box E3 ubiquitin ligase	*OsTUD1*	*tud1*	3	Hu et al. (2013)
	BU1	Helix–loop–helix protein	*OsBU1*	*OsBU1 RNAi*	6	Tanaka et al. (2009)
	PRA2	Small G protein	*OsPRA2*[a]	*35S::OsPRA2*	6	Zhang et al. (2016)
	OFP	OVATE family protein	*OsOFP8*	*OsOFP8 RNAi*	1	Yang et al. (2016)
	RLA1/SMOS1	APETALA2 transcription factor	*OsRLA1/OsSMOS1*	*Rla1*	5	Qiao et al. (2017)
	–	–	*OsSG1*[a]	*35S::OsSG1*	9	Nakagawa et al. (2012)
	XIAO	LRR kinase	*OsXIAO*	*Xiao*	4	Jiang et al. (2012)
	SDG725	H3K36 methyltransferase	*OsSDG725*	*sdg725*	2	Sui et al. (2012)
	–	–	*OsBLE3*	*OsBLE3 antisense*	5	Yang et al. (2006)

[a]It is a negative regulated gene in the pathway

[b]The phenotype of mutant or transgenic plant is tall stem

In *Arabidopsis*, BR directly interacts with BRI1 and BAK1 to form a BRI1–BR–BAK1 complex on the cell surface. Sequential transphosphorylation between BRI1 and BAK1 activates BRI1, which then phosphorylates BSKs/CONSTITUTIVE DIFFERENTIAL GROWTH 1 (CDG1). The active BSKs/CDG1 phosphorylates BSU1, which dephosphorylates and inactivates BRASSINOSTEROID INSENSITIVE 2 (BIN2). BZR1 and BRI1 EMS SUPPRESSOR 1 (BES1)/BRASSINAZOLE RESISTANT 2 (BZR2) are dephosphorylated by PP2A and move into the nucleus to induce expression of *PACLOBUTRAZOL-RESISTANT 1 (PRE1)*, but repress *ILI1 BINDING bHLH 1* (*IBH1*) expression. PRE1, IBH1 and HOMOLOG OF BEE2 INTERACTING WITH IBH1 (HBI1) form an antagonistic cascade to regulate plant growth. SUPPRESSOR OF BRI 1 (SBI1) is involved in the deactivation of BRI1 through methylation of PP2A (Wang et al. 2012; Zhang et al. 2014a) (Fig. 6). BRI1 is negatively feedback

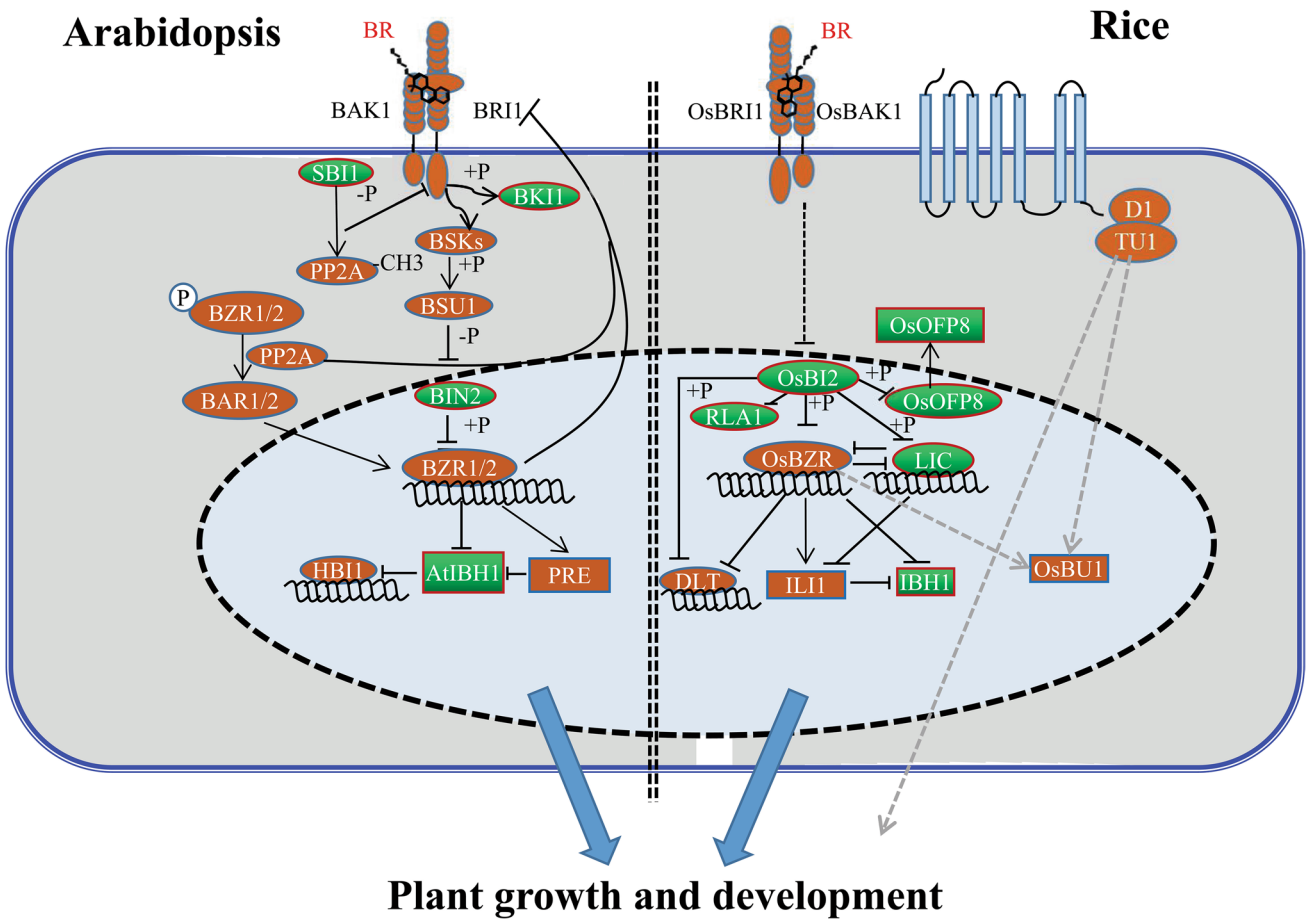

Fig. 6 BR-signaling pathways in rice and *Arabidopsis*. The left panel shows the BR signal transduction pathway in *Arabidopsis*, while the right panel shows that in rice. Orange indicates that the components play positive roles in BR signaling, whereas green indicates that components play negative roles, and a gray dotted line indicates a scenario to be verified (Tong and Chu 2012; Zhang et al. 2014a; Yang et al. 2016; Qiao et al. 2017). In rice, BR binding to BR receptor *Oryza sativa* BRASSINOSTEROID INSENSITIVE 1 (OsBRI1) promotes association with*Oryza sativa* BRI1 ASSOCIATED KINASE 1 (OsBAK1), and inactivates *Oryza sativa* GLYCOGEN SYNTHASE KINASE3-LIKE GENE 1 (OsGSK1)/BRASSINOSTEROID INSENSITIVE 2 (OsBIN2) via an unknown mechanism. OsGSK1/OsBIN2 phosphorylates OsBZR1, LIC and DLT, and inhibits their activity. *OsBZR1* induces the expression of *ILI1*, but represses the expression of *IBH1*, *TILLER ANGLE INCREASED CONTROLLER* (*LIC*) and *DWARF AND LOW TILLERING* (*DLT*), whereas *LIC* represses the expression of *OsBZR1*. Like OsBZR1, OsLIC interacts with and is phosphorylated by OsGSK1/OsBIN2 in order to be retained in the cytoplasm. BR treatment inhibits OsGSK1 activity, thereby inducing OsLIC dephosphorylation and transfer of OsLIC to the nucleus. Nuclear-located OsLIC directly binds to the OsBZR1 promoter, and represses OsBZR1 transcriptional activity. Thus, OsLIC and OsBZR1 represent a pair of antagonistic transcription factors that repress each other during transcription, and their repression strength may depend on the BR level. OsBZR1 promotes signaling in the presence of low levels of BR, whereas OsLIC represses BR signaling predominantly at high levels of BR. Thus, the dynamics of BR responses in rice development are modulated by a positive regulator, OsBZR1, and a negative regulator, OsLIC (Wang et al. 2008; Zhang et al. 2012). Additionally, the heterotrimeric G-protein α subunit, encoded by rice *d1* mutant defective gene RICE HETEROTRIMERIC G PROTEIN ALPHA 1 (*OsRGA1*) and mentioned in the GA pathway before, is involved in another BR-signaling pathway, in which D1/RGA1 and TAIHU DWARF 1 (TUD1) act together to mediate BR signaling (Oki et al. 2009). *Oryza sativa* OVATE family proteins (OsOFP8) and reduced leaf angle 1 (RLA1)/small organ size 1 (SMOS1) functions as a positive regulator. OsOFP8 is interacted with and phosphorylated by OsGSK2/OsBIN2, thus shuttles from nuclear to the cytoplasm and is targeted for proteasomal degradation (Yang et al. 2016). RLA1/SMOS1 can interact with OsBZR1 to enhance its transcriptional activity. OsGSK2/OsBIN2 can interact with and phosphorylate RLA1/SMOS1 to reduce its stability (Qiao et al. 2017). BR-signaling pathway in *Arabidopsis* is indicated in text

regulated by BZR1 and BES1 at the transcriptional level (Sun et al. 2010; Yu et al. 2011), and BRI1 is also negatively feedback regulated by PP2A at the protein level (Di Rubbo et al. 2011; Wu et al. 2011). In addition, there is a lateral organ boundaries (LOB)-BR feedback loop that limits growth in the organ boundaries. *LOB* is positively regulated by BRs and is expressed in organ boundaries where it activates expression of PHYB ACTIVATION TAGGED SUPPRESSOR 1 (BAS1), which inactivates BR (Diaz 2016).

In rice, *OsBRI1* is the counterpart of the *Arabidopsis* gene *BRI1*, which is a cell surface receptor kinase and can perceive the extracellular BR signal. Its loss-of-function mutant, *d61*, was the first identified BR-insensitive mutant in rice and has erect leaves and dwarf culms (Yamamuro et al. 2000). OsBAK1 (also named *Oryza sativa* SOMATIC EMBRYOGENESIS RECEPTOR KINASE 1 (OsSERK1) can interact with OsBRI1 and overexpression of a truncated intracellular domain of *OsBAK1* caused BR hypersensitivity and partially suppressed mutant phenotypes of the *Arabidopsis bri1-5* and rice *d61-1* genes (Wang et al. 2007; Li et al. 2009). OsGSK1 and GLYCOGEN SYNTHASE KINASE3-LIKE GENE 3 (GSK3)/SHAGGY-LIKE KINASE (GSK2) (united as OsBIN2 in Fig. 6) are homologues to *Arabidopsis BRASSINOSTEROID INSENSITIVE 2* (*AtBIN2*) and act as negative regulators of rice BR signaling and stress responses (Koh et al. 2007; Tong and Chu 2012). Overexpression of *OsGSK1* in *Arabidopsis* results in a similar dwarf phenotype to the gain-of-function mutant *bin2-1* in *Arabidopsis*. The T-DNA knockout mutant of *OsGSK1* is more tolerant to heat, cold, salt and drought stresses (Koh et al. 2007). *OsBZR1* is a positive regulator of BR signaling and suppression of *OsBZR1* by RNAi causes semi-dwarfism, erect leaves and BR-insensitive phenotypes (Bai et al. 2007; Table 2).

OsLIC, which encodes a novel CCCH-type zinc finger protein, has a negative regulatory role on the BR signal. Antisense-mediated suppression of *OsLIC* results in larger leaves and tillering angles and decreased numbers of seeds, while a gain-of-function mutant of *OsLIC* leads to erect leaves and reduced BR sensitivity (Wang et al. 2008; Zhang et al. 2012). *OsDLT*, encoding a plant-specific GRAS family protein, acts downstream to positively regulate BR responses, and mutants of this gene exhibit a compact semi-dwarf stature, dark-green erect leaves, reduced tillering and late flowering. OsBZR1 directly binds to the promoter of the *OsDLT* gene and suppresses its transcription (Tong et al. 2009). OsDLT can also physically interact with and is phosphorylated by OsGSK2 (Tong et al. 2009). *Oryza sativa* INCREASE LEAF INCLINATION 1 (OsILI1) and OsIBH1 are likely to regulate rice leaf angle by antagonistically interacting with each other, and OsBZR1 directly binds to their promoter to induce *OsILI1*, but represses *OsIBH1* expression (Zhang et al. 2009; Table 2).

Rice D1/RGA1, known to be involved in GA signaling (Ueguchi-Tanaka et al. 2000; Suharsono et al. 2002), was also suggested to be a BR-signaling component (Wang et al. 2006; Oki et al. 2009). *d1*, the loss-of-function mutant of *D1/RGA1*, is less sensitive to BL and produces plants with longitudinally compressed seeds, dense panicles, erect leaves and a dwarf phenotype (Wang et al. 2006; Oki et al. 2009). Moreover, *RGA1* may be involved in a distinct BR signaling pathway from *OsBZR1* (Oki et al. 2009). Hu et al. (2013) reported that *D1* directly interacts with *TUD1*, which encodes a U-box E3 ubiquitin ligase, to mediate BR signaling. The dwarf phenotype of the *tud1* mutant is mainly due to decreased cell proliferation and disorganized cell patterns in the aerial organs. Various analyses by genetic, phenotypic and physiological methods have shown that *tud1* is epistatic to *d1* and is less sensitive to BR treatment (Hu et al. 2013) (Table 2, Fig. 6). Tanaka et al. (2009) identified a novel BR-induced gene *BRASSINOSTEROID UPREGULATED 1* (*BU1*), which encodes a helix–loop–helix protein. Rice plants that overexpress *BU1* have more pronounced bending of the lamina joint and larger grains and plants in which *BU1* has been knocked-out by RNAi have erect leaves. BU1 expression is weaker in both *d61* and *d1* mutants. The BU1 protein is, therefore, a positive regulator of the BR response and participates in two BR signaling pathways through OsBRI1 and RGA1 (Tanaka et al. 2009) (Table 2, Fig. 6). Zhang et al. (2017) showed that a rice small G protein OsPRA2 (homologous with Pea Pra2 protein) plays a repressive role in the BR signaling pathway by inhibiting dephosphorylation of OsBZR1 and thus inhibiting its function. OsPRA2 co-localized with, and directly bound to OsBRI1 at the plasma membrane, which not only inhibited OsBRI1 autophosphorylation, but also inhibited the phosphorylation of OsBAK1 mediated by OsBRI1 (Zhang et al. 2017).

The transcription factor OsOFP8 is an OVATE FAMILY PROTEIN (OFP) that plays a positive role in BR signaling. OsOFP8 is suggested to be phosphorylated by OsGSK2, the counterpart of Arabidopsis BIN2. Phosphorylated OsOFP8 shuttles from nucleus to the cytoplasm and is targeted for proteasomal degradation (Yang et al. 2016). Qiao et al. (2017) reported another gene, *REDUCED LEAF ANGLE 1* (*RLA1*), which is identical to the previously reported *SMALL ORGAN SIZE 1* (*SMOS1*) induced by IAA (Aya et al. 2014) and encodes a transcription factor with an APETALA2 DNA-binding domain. RLA1/SMOS1 functions as a positive regulator in the BR signaling pathway and can interact with OsBZR1 to enhance its transcriptional activity. GSK2 can interact with and phosphorylate RLA1/SMOS1 to reduce its stability.

There are several other genes involved in the BR signaling pathway with unclear functions. Nakagawa et al. (2012) identified a *Short-grain* 1 (*Sg1*) dominant mutant from rice activation-tagged lines. Overexpression of *SG1* in rice results in a dwarfed plant with broad, dark-green, erect leaves, short grains and insensitivity to brassinolide in the lamina inclination assay (Nakagawa et al. 2012). Another gene, *XIAO*, is predicted to encode an LRR kinase in rice, and the T-DNA insertion mutant *xiao* displays dwarfism and erect leaves, together with lower seed set. The smaller stature of *xiao* plants is due to a reduced cell division rate and the BR response is enhanced in certain roots and the coleoptile, even though the BR levels are reduced at the

whole-plant level. Therefore, *XIAO* may provide a possible connection between BR signaling and cell-cycle regulation during organ growth (Jiang et al. 2012). *SDG725*, a member of SET DOMAIN GROUP (SDG) proteins, encodes a H3K36 methyltransferase in rice and its knockdown leads to dwarfism, shortened internodes, erect leaves and smaller seeds. *SDG725* depletion results in down-regulation of BR signal-related genes, including *D11*, *BRI1* and *BU1* (Sui et al. 2012). *Oryza sativa BRASSINOLIDE-ENHANCED GENE 3* (*OsBLE3*) is a BL up-regulated gene and the BL signal that leads to enhanced expression of *OsBLE3* is mediated, at least in part, through *OsBRI1*. In *OsBLE3* antisense transgenic rice plants, growth is retarded and internode cell length is about 70% of that in the control lines. Moreover, it indicates that *OsBLE3* is involved in cell elongation through dual regulation of BL and IAA (Yang et al. 2006; Table 2).

SL-related pathways

SLs are a group of terpenoid lactones with high structural diversity. SLs were first known for their function in rhizosphere signaling (Akiyama et al. 2005). More recently, they have been identified as inhibitors of shoot branching (Gomez-Roldan et al. 2008; Umehara et al. 2008; Domagalska and Leyser 2011; Ruyter-Spira et al. 2013; Wen et al. 2015), regulating mesocotyl elongation, stem secondary growth, leaf senescence, seed germination and root development (Ruyter-Spira et al. 2013; Hu et al. 2014; Sun et al. 2015; van Zeijl et al. 2015). Deficiencies in SL production and perception lead to greater shoot branching and reduced rice plant height (Domagalska and Leyser 2011; Ruyter-Spira et al. 2013). Shoot branching plays an important role in determining plant architecture. Tillering is a specialized branch in rice, which is crucial to rice productivity, but its molecular regulation is poorly understood (Wen et al. 2015). Studies with branching mutants have identified key players in SL biosynthesis and signaling.

Genes involved in SL biosynthesis The SL biosynthesis pathway, beginning with all-*trans*-β-carotene and finishing with *ent*-20-epi-5-deoxystrigol, is illustrated in Fig. 7 (Harrison et al. 2015). Rice mutants *dwarf 27* (*d27*), *high tillering dwarf 1* (*htd1*)/*semi dwarf-t* (*sd-t*)/*dwarf 17* (*d17*), *dwarf 10* (*d10*), which have defective in *D27*, *Oryza sativa CAROTENOID CLEAVAGE DIOXYGENASE 7* (*OsCCD7*) and *Oryza sativa CAROTENOID CLEAVAGE DIOXYGENASE 8* (*OsCCD8*) genes, respectively, have reduced SL levels, implying roles in the SL biosynthetic pathway (Umehara et al. 2008; Gomez-Roldan et al. 2008; Lin et al. 2009; Table 3). D27 is a β-carotene isomerase, which works upstream of *CCD7* and *CCD8* in the biosynthetic pathway (Alder et al. 2012; Waters et al. 2012). *OsCCD7* and *OsCCD8* are homologous to the *Arabidopsis MORE AXILLARY GROWTH 3 (MAX3)/CCD7* and *MAX4* genes, respectively, which sequentially cleave carotenoid precursors to produce carlactone. A rice cytochrome P450 CYP711 subfamily member (homologous to Arabidopsis *MAX1*) then acts as a carlactone oxidase to stereoselectively convert carlactone into *ent*-2′-epi-5-deoxy-strigol (Zhang et al. 2014b; Table 3). In mutant *d27* roots, SLs are undetectable in the root secretions, leading to a high tillering and dwarfed phenotype. This mutant is considered SL-defective as applications of SLs can restore the wild-type phenotype (Lin et al. 2009). In *htd1* mutants, the removal of axillary buds can increase height, indicating that the dwarf phenotype results from excessive tillering (Zou et al. 2005). *d10* is an enhanced branching rice mutant, with reduced apical dominance (Arite et al. 2007).

Genes involved in SL signaling SL signaling requires the hormone-dependent interaction of DWARF 53 (D53) with DWARF 14 (D14), a probable candidate SL receptor, and DWARF 3 (D3), an F-box component of the SCF E3 ubiquitin ligase complex (Jiang et al. 2013) (Fig. 8a). A model of the OsMADS57 (transcription factors of the MADS-domain

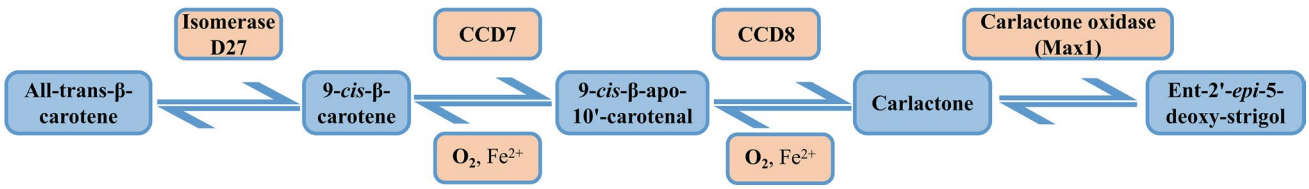

Fig. 7 The strigolactone (SL) biosynthesis pathway from all-*trans*-β-carotene to *ent*-20-epi-5-deoxystrigol. The biosynthetic pathway of SLs begins with the isomerization of all-*trans*-β-carotene to 9-*cis*-β-carotene, a reaction that is catalyzed by β-carotene isomerase D27 (Lin et al. 2009; Alder et al. 2012). Oxidative cleavage of 9-*cis*-β-carotene at the 9′, 10′ position is then catalyzed by carotenoid cleavage dioxygenase 7 (CCD7), to produce 9-*cis*-β-apo-10′-carotenal (Alder et al. 2012). Carotenoid cleavage dioxygenase 7 (CCD8) catalyzes an unusual double oxygenation of 9-*cis*-b-apo-10′-carotenal to produce an intermediate known as carlactone (Alder et al. 2012). Carlactone is then oxidized by consecutive P450 enzyme oxidations to give *ent*-2′-epi-5-deoxy-strigol, the presumed precursor of rice SLs: recombinant *Arabidopsis* Max1 has been shown to form carlactonoic acid (Abe et al. 2014), whereas a recombinant Max1 homologue from *Oryza sativa* (called carlactone oxidase) has been shown to form *ent*-2′-epi-5-deoxystrigol directly (Zhang et al. 2014b)

Table 3 Dwarf genes involved in strigolactone (SL) biosynthesis and signal transduction in rice

Pathway	Enzyme name	Gene product	Gene name	Mutant/transgenic name	Chrom. location	References
SL biosynthesis	–	β-carotene isomerase	*OsD27*	*d27*	11	Lin et al. (2009), Alder et al. (2012)
	CCD7	Carotenoid cleavage dioxygenase 7	*OsCCD7/D17/HTD1*	*htd1/sd-t/d17*	4	Zou et al. (2005, 2006)
	CCD8	Carotenoid cleavage dioxygenase 8	*OsCCD8/D10*	*d10*	1	Ishikawa et al. (2005), Arite et al. (2007), Zhang et al. (2010), Yuan et al. (2013)
	CYP711	Carlactone oxidase	*OsMAX1*	–	1	Zhang et al. (2014b)
SL signal	–	F-box leucine-rich repeat protein	*OsD3*	*d3*	12	Ishikawa et al. (2005), Yasuno et al. (2007)
	–	Hydrolase/esterase	*OsHTD2/OsD88/ OsD14*	*htd2/d88/d14*	3	Gao et al. (2009); Liu et al. (2009)
	–	Hydrolase/esterase	*OsD14L*	*OsD14L RNAi*	3	Yoshida et al. (2012); Kameoka and Kyozuka (2015)
	–	Double Clp-N motif-containing P-loop nucleoside triphosphate hydrolase	*OsD53*	*d53*	11	Jiang et al. (2013)
	–	TCP transcription factor	*OsTB1/OsFC1*	*tb1/fc1*	3	Guo et al. (2013), Xu et al. (2015)
	–	–	*OsMADS57*[a]	*35S::OsMAD57*	2	Guo et al. (2013)

[a]It is a negative regulated gene in the pathway

family)-mediated network for the control of tillering, as proposed by Guo et al. (2013), is shown in Fig. 8b.

Some genes responsible for the dwarf and multi-tillering phenotypes of rice are involved in the SL signaling pathway (Ishikawa et al. 2005; Zou et al. 2006; Arite et al. 2007; Lin et al. 2009; Table 3). *D3* is homologous to the *Arabidopsis MAX2/ORESARA 9* (*ORE9*) and is involved in tillering and shoot branching (Ishikawa et al. 2005). Recently, a rice mutant *high-tillering dwarf 2* (*htd2*) was used to identify the *D14/DWARF 88* (*D88*)*/HTD2* gene, which encodes a novel putative rice hydrolase/esterase and is involved in SL perception or downstream metabolism (Liu et al. 2009; Gao et al. 2009; Leyser 2009; Beveridge and Kyozuka 2010). D14-LIKE (D14L), a homolog of D14, acts similarly to inhibit mesocotyl elongation and functions via an unknown SL independent pathway (Yoshida et al. 2012; Kameoka and Kyozuka 2015). Jiang et al. (2013) described a dominant SL-insensitive rice mutant *d53*, which exhibits a dwarf and prolific tillering phenotype and using this mutant, cloned the *D53* gene, which encodes a substrate of the SCF^{D3} ubiquitination complex and functions as a repressor of SL signaling. Like the *d3* mutant, *d53* is resistant to exogenous applications of SLs. Xu et al. (2015) found that the rice gene *Oryza sativa TEOSINTE BRANCHED 1* (*OsTB1*)*/Oryza sativa FINE CULM 1* (*OsFC1*) is required for bud inhibition and is transcriptionally regulated in axillary buds in rice. *OsTB1/OsFC1* is a downstream component of the SL signaling pathway. Cytokinin (CK) and SL rapidly reduce and increase the expression of *OsTB1/OsFC1* in the buds, respectively, implying that FC1 might be a common target for the CK and SL pathways. The rice mutant *tb1/fc1* has greater tillering, which is similar to *d14* and the activation-tagged mutant *osmads57-1*, whereas *osmads57-1* has a very weak dwarf phenotype. *OsMADS57* is predicted to encode a protein containing a MADS-box domain. *OsMADS57* overexpression transgenic lines have increased tillering, while *OsMADS57* antisense transgenic lines have reduced tillering (Guo et al. 2013; Table 3).

Genes involved in IAA biosynthesis and signaling

IAA is the predominant auxin in plants and plays an important role in many processes during plant growth and development, including cell division, differentiation and elongation, flower and vascular development, tropism and embryogenesis (Vanneste and Friml 2009). The tryptophan biosynthetic pathway is considered to be one of the critical steps in IAA biosynthesis (Zazimalova and Napier 2003). *Tryptophan-deficient dwarf1* (*tdd1*), a rice IAA-deficient mutant, is embryonic lethal, and the regenerated *tdd1* plants exhibit dwarfing, narrow leaves and abnormal flowers. *TDD1* encodes an anthranilate synthase β-subunit and

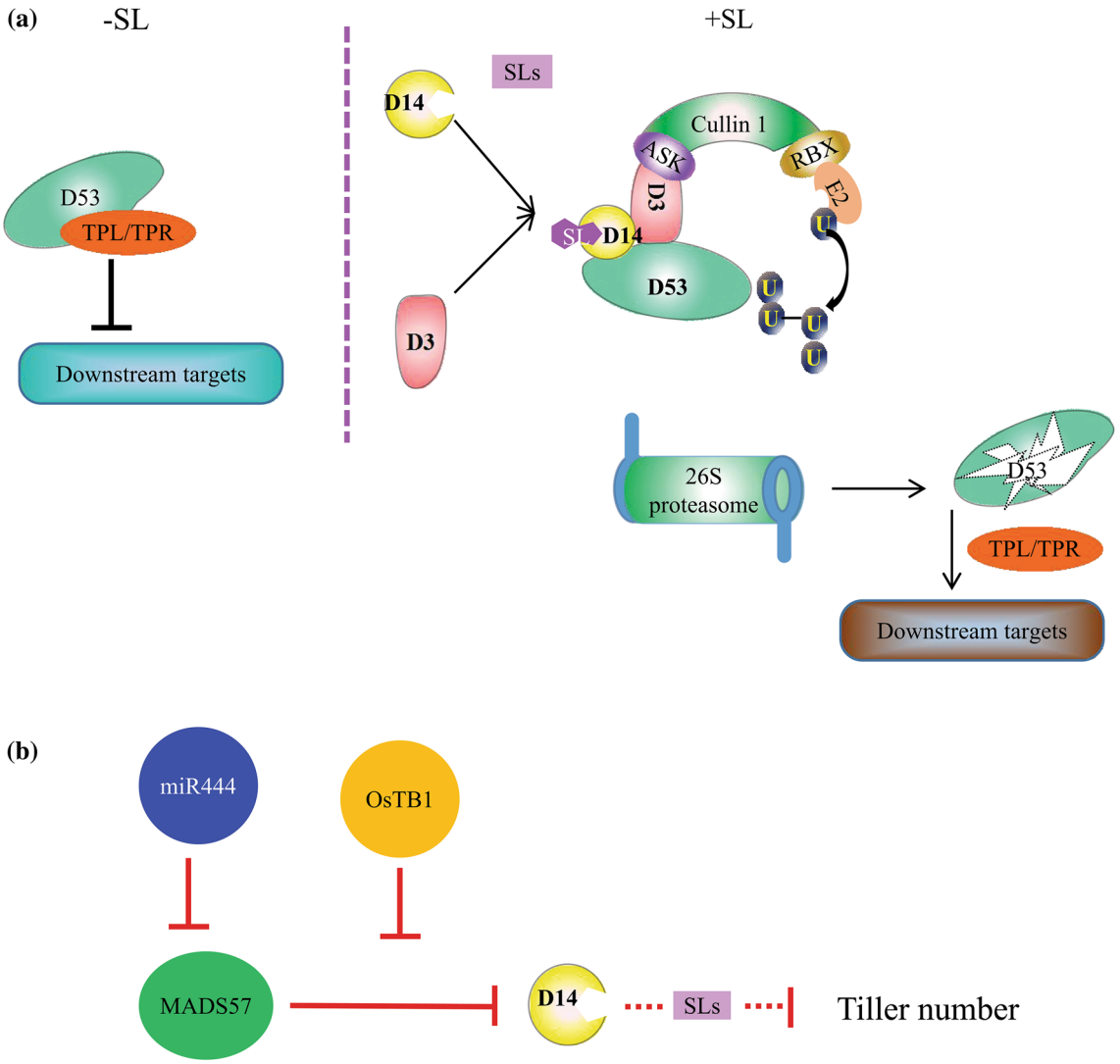

Fig. 8 Model of the SL signaling pathway. **a** A proposed SL signaling pathway that involves SL-dependent degradation of the DWARF 53 (D53) repressor, mediated by the D14–D3 complex (Jiang et al. 2013). In the absence of SLs, D53 is stable and recruits TOPLESS (TPL) or TPL-RELATED PROTEINS (TPRs), which are transcriptional co-repressors, and repress downstream responses. In the presence of SLs, perception of SL leads to SCF^{D3}-mediated ubiquitination of D53 and its subsequent degradation by the proteasome system, in a manner that requires D14 and the SCF^{D3} ubiquitin ligase, which in turn releases the repression of downstream responses (Jiang et al. 2013). **b** Model of the OsMADS57 (transcription factors of the MADS-domain family)-mediated network for control of tillering (Guo et al. 2013). OsMADS57 is predicted to be a target of the 21-nt noncoding RNA *miR444a*, and *OsMIR444a*-regulated *OsMADS57*, together with *Oryza sativa TEOSINTE BRANCHED 1* (*OsTB1*), which is synonymous with *FINE CULM 1* (*FC1*), target *DWARF 14* (*D14*) to control tillering. OsMADS57 binds to the promoter and directly suppresses D14 expression, and interaction of *OsMADS57* with *OsTB1* reduces *OsMADS57* inhibition of *D14* transcription (Guo et al. 2013)

works upstream of Trp-dependent IAA biosynthesis (Sazuka et al. 2009; Table 4).

Aux/IAA proteins are short-lived transcriptional regulators, which can interact with ARF transcription factors by preventing them from binding to the promoters of auxin-responsive target genes, thus repressing the auxin response (Song et al. 2009). *OsIAA1* is a member of *Aux/IAA* family in rice and its transcription is induced by various phytohormones including IAA. Overexpression of *OsIAA1* in rice results in reduced auxin sensitivity but increased sensitivity to BR. Furthermore, *OsIAA1*-overexpressing transgenic plants have decreased plant height and loose plant architecture. Yeast two-hybrid analysis suggests that OsIAA1 interacts with OsARF. A T-DNA insertion mutant of *OsARF1* is less sensitive to BR application and resembles the phenotype of *OsIAA1*-overexpression plants (Song et al. 2009). Therefore, OsIAA1–OsARF1 could play a critical role in mediating the auxin and BR signal pathways (Table 4).

Table 4 Dwarf genes in rice involved in pathways other than those relating to giberellins, brassinosteroids or strigalactones

Pathway	Enzyme name	Gene product	Gene name	Mutant/transgenic name	Chrom. location	References
IAA biosynthesis	–	Anthranilate synthase β-subunit	*OsTDD1*	*tdd1*	4	Sazuka et al. (2009)
Cross-talk of IAA and BR signaling	–	Nuclear protein	*OsIAA1*[a]	*ubi::OsIAA1*	1	Song et al. (2009)
	–	Transcription factor	*OsARF1*	*osarf*	1	Song et al. (2009)
ABA/GA balance	AP2	APETALA-2-Like Transcription Factor	*OsAP2-39*	*35S::OsAP2-39*	4	Yaish et al. (2010)
Cross talk between ETH and GA signaling	AP2/ERF	Ethylene-responsive element binding factor	*OsEATB*[a]	*35S:OsEATB*	9	Qi et al. (2011)
Crosstalk between JA and GA signaling	COI1	The F-box protein coronatine insensitive 1	*OsCOI1a*[a] and *OsCOI1b*[a]	*coi1 RNAi*[b]	1 and 5	Yang and He (2012)
Interlink between ABA and BR signaling	*REM4.1*	Remorin protein	*OsREM4.1*[a]	*35S::OsREM4.1*	7	Gui et al. (2016)
Cell wall biosynthesis in response to GA and BR	–	Membrane-bound endo-1,4-β-D-glucanase	*OsGLU1*	*glu*	3	Zhou et al. (2006)
Cell wall development response to GA	CD1	Cellulose synthase-like D	*OsCD1*	*cd1*	12	Luan et al. (2011)
Cell wall development	CESA	Cellulose synthase catalytic subunit	*OsCesA4*	*oscesa4*	1	Tanaka et al. (2003)
	CESA	Cellulose synthase catalytic subunit	*OsCesA7*	*oscesa7*	10	Tanaka et al. (2003)
	CESA	Cellulose synthase catalytic subunit	*OsCesA9*	*oscesa9*	9	Tanaka et al. (2003)
Cytosolic glutamine synthetic pathway	GS1;1	Cytosolic glutamine synthetase	*OsGS1;1*	*osgs1;1*	2	Tabuchi et al. (2005)
RNA editing	OGR1	Pentatricopeptide repeat-DYW protein	*OsOGR1*	*ogr1*	2	Kim et al. (2009)
Cell division	–	–	*OsSSD1*	*ssd1*	3	Asano et al. (2010)
Ubiquitin–proteasome pathway	–	U-box domain containing protein	*OsD162(T)*	*d162(t)*	3	Zhang et al. (2011)
Fatty acid metabolism	FAD	ω-3 fatty acid desaturase	*OsFAD8*	*1B-10014*	7	Liu et al. (2012)
	CYP96B4	P450 monooxygenases	*OsSD37*	*sd37*	3	Zhang et al. (2014c)
Unknown pathway	OSH15	Kn1-type of the homeobox transcription factors	*OSH15*	*d6*	7	Sato et al. (1999)
	–	–	*OsHTD3*	*htd3*	12	Zhang et al. (2011)
	–	Lissencephaly type-1-like protein	*OsLIS-L1*	*oslis-l1*	8	Gao et al. (2012)
	–	–	*DWT1*	*dwt1*	1	Wang et al. (2013a)

[a]It is a negative regulated gene in the pathway

[b]The phenotype of mutant or transgenic plant is tall stem

Genes involved in interactions between the other relevant dwarfing phytohormones

The interplay of phytohormones controls plant growth and developmental processes. *Oryza sativa APETALA 2* (*OsAP2*)*-39* encodes an APETALA-2-like transcription factor and overexpression of this gene leads to a dwarfed, lower yielding phenotype. In vitro and in vivo analyses have demonstrated that transcription of the ABA biosynthesis gene *Oryza sativa 9-CIS-EPOXYCAROTENOID DIOXYGENASE-1* (*OsNCED-I*) and the GA catabolism gene *EUI* is directly controlled by *OsAP2-39*. *OsAP2-39* is, therefore, likely to regulate the ABA/GA balance in rice, which in turn affects plant growth and seed production (Yaish

et al. 2010). Qi et al. (2011) also demonstrated that *Oryza sativa ERF PROTEIN ASSOCIATED WITH TILLERING AND BRANCHING* (*OsEATB*), a rice AP2/ETHYLENE-RESPONSIVE ELEMENT BINDING FACTOR (*ERF*) family gene, restricts ethylene-induced enhancement of GA responsiveness during internode elongation, by down-regulating a GA biosynthetic gene *CPS*. Transgenic plants overexpressing *OsEATB* have a dwarfed phenotype, indicating that the internodal elongation process is suppressed by cross-talk between ETH and GA (Qi et al. 2011). The *F-BOX PROTEIN CORONATINE INSENSITIVE 1* (*COI1*) encodes a component of the SCF E3 ubiquitin ligase and receptor of JA (Xie et al. 1998; Katsir et al. 2008; Fonseca et al. 2009; Yan et al. 2009). The rice genome contains two closely related *COI1* genes, *OsCOI1a* and *OsCOI1b*, both involved in crosstalk between the JA and GA signaling pathways in defense against biotic and abiotic stresses (Yang and He 2012). *Oryza sativa REMORIN 4.1* (*OsREM4.1*) gene is transcriptionally regulated by ABA and functions as an OsBRI1 substrate and OsSERK1-interacting protein. This inhibits the formation and subsequent activation of the OsBRI1–OsSERK1 receptor complex, explaining the antagonistic interactions between ABA and BRs that are coordinated in rice (Gui et al. 2016). *OsGLU1* encodes a putative membrane-bound endo-1,4-β-D-glucanase and plays an important role in plant cell development. The expression of *OsGLU1* is induced by GA and BR, suggesting that it is a component of the GA and BR signaling pathways related to cell wall development. The dwarf mutant *glu* has reduced cell elongation, and altered cell wall composition, affecting internode elongation (Zhou et al. 2006; Table 4).

Genes related to non-hormone pathways

There are many genes controlling plant height from a range of other pathways besides the GA, BR, SL and IAA-related pathways. This includes those relating to cell wall development, the cytosolic glutamine synthetic pathway, RNA editing, cell division, the ubiquitin–proteasome pathway and fatty acid metabolism (Table 4). In addition to dwarfing, mutations to these genes cause other traits, such as a brittle culm, poor fertility, narrow and curled leaves and short spikes.

The cell wall plays an important role in plant architecture and morphogenesis. *Oryza sativa CURLED LEAF AND DWARF 1*(*OsCD1*) is a member of the *CELLULOSE SYNTHASE-LIKE D* (*CSLD*) subfamily and is involved in cell wall formation. The rice dwarf mutant *cd1* has a defective version of this gene, causing a significant reduction in the cellulose and xylose content of the mature culm. Mutant and wild-type plants all exhibit a constitutive response to GA3, suggesting a mode of action other than phytohormone signal transduction (Luan et al. 2011). Tanaka et al. (2003) found three *CELLULOSE SYNTHASE CATALYTIC SUBUNIT* (*CesA*) genes (*OsCesA4*, *OsCesA7* and *OsCesA9*), and mutation of these genes by Tos17 retrotransposon insertion resulted in a brittle/thin culm, semi-dwarf and low-fertility phenotype. Furthermore, it is indicated that there are no functional overlaps among these genes; therefore, they may form a complex involved in the synthesis of the cell wall (Tanaka et al. 2003; Table 4).

Oryza sativa GLUTAMINE SYNTHETASE 1;1 (*OsGS1;1*) gene encodes a cytosolic glutamine synthetase, and Tos17 retrotransposon insertional mutants have retarded growth rates, smaller panicles and inhibited grain filling (Tabuchi et al. 2005). A rice mutant *opaque and growth retardation 1* (*ogr1*), defective in seven specific RNA editing sites on five mitochondrial transcripts, displays dwarfism and sterility phenotypes. *ogr1*, the T-DNA insertion mutant of the *OGR1* gene, encodes a pentatricopeptide repeat protein containing a DYW motif (Kim et al. 2009). The phenotype of the dwarf mutant *sword shape dwarf 1* (*ssd1*) exhibits defects in the elongation of various organs, different from typical GA- or BR-related dwarf phenotypes. *SSD1* encodes a plant-specific protein of unknown function and probably controls plant growth by regulating cell division (Asano et al. 2010). The single recessive gene, *dwarf 162(t)* (*d162(t)*), causes dwarfing of rice and has been mapped to chromosome 3. The candidate gene is considered to encode a U-box domain containing protein, which plays an important role in maintaining cellular homeostasis (Zhang et al. 2011). *Oryza sativa FATTY ACID DESATURASE* (*OsFAD8*) encodes rice chloroplast ω-3 fatty acid desaturase and its expression is induced at low temperatures. *OsFAD8* T-DNA knockout plants are shorter and have lower levels of trienoic fatty acids after exposure to cold temperatures. *OsFAD8* may, therefore, have a role in cold tolerance (Liu et al. 2012). The rice semi-dwarf mutant *semi dwarf 37* (*sd37*), a novel GA/BR independent mutant, is defective in CYP96B4, which is an important regulator of plant growth. *sd37* has smaller leaves, panicles and seeds due to a decrease in cell number, especially in the shoots (Zhang et al. 2014c; Table 4).

Genes involved in uncharacterized pathways

The *Oryza sativa HOMEOBOX 15* (*OSH15*) gene is a member of the knotted1-type homeobox gene family and plays a role in the development of internodes by influencing cell division and elongation. Internodes of the *OSH15* loss-of-function mutant *d6* have abnormally shaped epidermal and hypodermal cells and unusually arranged small vascular bundles (Sato et al. 1999). The *high-tillering dwarf 3* (*htd3*) mutant, which is caused by the single recessive gene *HTD3*, has a greater number of tillers and a shorter culm. *HTD3* has been mapped within 3100 kb of the centromere of chromosome 12, but the identity of this gene has yet to

be uncovered (Zhang et al. 2011). *Oryza sativa LISSENCEPHALY TYPE-1-LIKE 1* (*OsLIS-L1*) encodes a protein containing the WD40 motif and plays an important role in elongation of the first internode and male gametophyte formation in rice. The *oslis-l1* mutant has an abnormal developmental phenotype, including semi-dwarfing, a shorter panicle length and reduced male fertility (Gao et al. 2012). The *DWARF TILLER 1* (*DWT1*) locus regulates uniform growth of the main shoot and tillers in rice. The main shoot of the *dwt1* mutant is of nearly normal height at maturity but the tillers are dwarfed. Thirty-one putative open reading frames (ORFs) have been identified in the 197-kb genomic region covering the *DWT1* locus, but none are predicted to be involved in stem elongation or plant architecture. *DWT1* may represent a component of an unknown genetic pathway controlling the elongation of tiller culms in rice (Wang et al. 2013a, b; Table 4).

Future perspectives

Most dwarf genes are connected to phytohormone functions and there is a potential for farmers to control crop height using hormone antagonists or analogues. However, the application of chemicals to food crops may not be desirable in the future. Another strategy is to modify hormone content and homeostasis by genetic engineering or pyramiding breeding. Several studies have highlighted the huge potential of modulating expression of GA and BL biosynthesis and signaling genes in plant breeding (Divi and Krishna 2009; Huang et al. 2010). Tillering is crucial to rice productivity. Although there is limited evidence for SL-mediated tillering effects on yield traits, the strigolactone pathway is not fully elucidated and it could potentially be explored to improve productivity. Potential of modulating expression of genes involved in other hormones and non-hormones in plant breeding also remains to be explored.

How can dwarfing genes be better utilized in practice? In rice, for example, plant breeders have mainly utilized weak alleles of dwarf genes which are relatively free of adverse traits. *osdwarf4-1* has a slightly dwarfed stature and more erect leaves than the wild-type plant but no other phenotypic differences, which helps to increase grain yield, especially at a high planting density (Sakamoto et al. 2006). In more sophisticated approaches, dwarfing genes could be driven by tissue-specific promoters to ensure no undesirable pleiotropic effects. The advantages of targeted expression have been clearly demonstrated in rice (Sakamoto et al. 2003). When the rice GA-deactivation enzyme gene *GA2ox* is driven by the strong and constitutive actin promoter, the transgenic plants show severe dwarfing and significantly reduced grain set (Sakai et al. 2003). To avoid this problem, the *GA2ox* gene was coupled to the promoter of *OsGA3ox2* to ensure that GA deactivation only occurred in the vegetative tissues (Sakamoto et al. 2003). The outcome was semi-dwarfed plants with normal grain set, similar to plants containing the *sd1* gene. Alternatively, coupling the *DWARF4* gene to a vegetative tissue-specific promoter led to plants growing more vigorously than the wild-type with taller stature, better grain filling and larger seeds, leading to improved yields (Wu et al. 2008).

To better utilize crop height-related genes in practice, the following strategies are suggested: (1) As several metabolic pathways involving many genes control crop height, once new genes affecting crop height are identified, it will be necessary to clarify their functions by placing them in specific pathways or networks that regulate phytohormones or other developmental processes, including how they control crop height and whether they control other characteristics. (2) It will be necessary to learn how they interact with their up and downstream genes and determine the phenotype of double mutants. It is crucial to explore the key alleles in the metabolic pathways by assessing their impact on the phenotype in order to manipulate one or more genes to optimize the regulation of crop height. (3) It will be necessary to determine whether there is crosstalk between different hormone pathways, specifically whether common downstream targets exist.

Based on the above information, crop height genes can be divided into two categories depending on whether they have pleiotropic effects or not. If pleiotropic effects are beneficial, such as erect leaves, the genes can be used directly. If other effects are adverse, three strategies are suggested: (1) screen alleles of dwarf genes to ameliorate any pleiotropic adverse effects; (2) employ genome editing strategies for target specificity; (3) limit the expression of the dwarf genes to specific tissues using specific promoters, to avoid undesirable pleiotropic effects; (4) gradually reduce any adverse traits associated with dwarfing by crossing or back-crossing, using molecular markers to monitor inheritance of the dwarfing gene.

Once genes of interest in dwarfism and yield are identified, functional markers can be developed. This could be used to make a genotyping chip for crop height breeding, or as the basis for genome selection breeding. Crop height is one of the most important traits in crop ideotype breeding and each crop height-related gene behaves differently under certain environmental conditions (Botwright et al. 2005; Butler et al. 2005; Chapman et al. 2007; Rebetzke et al. 2012). Therefore, in order to use these genes appropriately, the impact of environmental factors such as light, temperature, water and nutrition needs to be ascertained. This is in agreement with the opinion that rice varieties with super high yield should have different ideal architecture characteristics in different ecological areas (Huang et al. 2009).

Rice is a model plant species, and research to investigate dwarfing will have implications for all crop species. It is also apparent that there are subtle differences between plant species in the metabolic pathways that control crop height, and these difference are expected to become more clear in future work. A multi-disciplinary approach involving plant genomics, physiology, metabolomics and breeding will be needed to untangle the complex genetic and environmental interactions that determine plant architecture. These investigations are so important for our looking ahead a different 'green revolution'.

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