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MINIREVIEW

Genes involved in the synthesis and signaling pathway of strigolactone, a shoot branching inhibitor

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Abstract

Branching is an important step in higher plant development, which not only determines the configuration of the plant directly, but also affects its adaptability to the environment. The interactions between hormones, genes, environmental and other factors subtly regulate the process of branching. Strigolactone is a newly recognized phytohormone and its content and distribution might be a key factor affecting branching. This review is focused on the genes related to synthesis and transduction pathway of strigolactone, and summarizes the inhibitory role of strigolactone in plant branching. Discussions about the issues to be clarified and prospects of the future research were also proposed.

Additional key words: auxin, axillary bud, carotenoid cleavage dioxygenase, cytokinin, feedback regulation.

Introduction

The plant shoots, established during post-embryogenesis, consists of primary stem derived from the primary shoot apical meristem and lateral shoots derived from axillary buds (McSteen and Leyser 2005). Axillary buds, located on the axil of a leaf, remain dormant before activating and then develop into branches or flowers (Beveridge 2006, Ongaro and Leyser 2008). Genetic, hormonal, and environmental signals precisely control these developmental processes. Shoot branching has a profound effect on the plant development (Schmitz and Theres 2005, Dun *et al.* 2006, Ongaro and Leyser 2008), resulting in the increase in adaptability to abiotic and biotic factors and in better utilization of resources (Ferguson and Beveridge 2009).

Classic theory of auxin depression of shoot branching demonstrates that the apex of the plant directly inhibits axillary bud outgrowth. When the apex is removed, the dormant axillary buds are activated and the plant starts branching (Thimann and Skoog 1934). However, subsequent research proved that this theory of the shoot branching is over-simplified. Firstly, "dormant" is a somewhat misleading term for the non-growing bud as such buds are highly metabolically active when producing a characteristic set of transcripts and proteins (Shimizu-Sato and Mori 2001). Secondly, direct application of auxin to buds does not inhibit their growth and apically applied auxin is not transported into the buds (Cline 1996). Furthermore, content of auxin in buds rise as they are activated (Cline 1996, Leyser 2003). At the same time, Turnbull *et al.* (1997) found that cytokinins (CKs) promote bud growth directly and their content increases as buds are activated. Consistent with this idea, basal supply of cytokinin through the transpiration stream released *Arbidopsis* buds from inhibition imposed by apical application of auxin (Chatfield *et al.* 2000). Taken together, auxin might regulate bud outgrowth and shoot branching by down-regulating cytokinin synthesis (Tanaka *et al.* 2006) and limiting cytokinin supply to the bud (Bangerth 1994).

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Abbreviations: CCD - carotenoid cleavage dioxygenase; CK - cytokinin; RMS - root-multiplication signal; SMS - shoot-multiplication signal.

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Mutants and new branching inhibitor

Mutants and reciprocal grafting experiments were made with the aim to understand the complex regulation processes of shoot branching. However, they brought us many complicated or even paradoxical questions. As concern *ramosus* (*rms*), *decreased apical dominance* (*dad)* and *more axillary growth* (*max*) mutants, the branching phenotype can be restored by grafting to wild-type rootstocks (Sorefan *et al.* 2003, Simons *et al.* 2007), while some wild-type shoots still exhibited wild-type branching when grafted to mutant rootstocks. The excessive branching of *max2* (Booker *et al.* 2005), *rms4* (Beveridge *et al.* 1996) and *dad2* (Simons *et al.* 2007) mutants would not be restored when grafted onto a wild-type rootstock. Thus, these mutants were defective in synthesis or response to a novel signal that was synthesized either in shoot or rootstock of wild-type (Foo *et al.* 2001, Ongaro and Leyser 2008). And once the signal is synthesized, it would move up from lower parts of stems or roots to axillary buds or node and inhibits shoot branching, maybe together with auxin (Beveridge *et al.* 2000).

Later Ongaro and Leyser (2008) proved that the compound mentioned above was neither auxin nor cytokinin. Meanwhile, Gomez-Roldan *et al.* (2008), and Umehara *et al.* (2008) revealed that various branching mutants in pea (*Pisum sativum*) and rice (*Oryza sativa*) showed a reduced contents of strigolactone, while a synthetic strigolactone analogue, GR24, was able to rescue a variety of branching mutants in different species including *Arabidopsis* (Tsuchiya and McCourt 2009). Furthermore, reciprocal grafting and double mutant studies demonstrated that the substances were in fact a kind of graft-transmissible, up-moving branching inhibitor. The novel hormone strigolactone, which is characterized by activity at low concentration and ability of long distance transport, seems to be critical for normal plant shoot development. Based on these findings, shoot-multiplication signal (SMS)/root-multiplication signal (RMS) pathways (Beveridge 2006, Dun *et al.* 2006) controlling shoot branching is likely to emerge.

Genes involved in the synthesis and signaling pathway of strigolactone

In SMS/RMS, a subset of orthologous genes like *MAX1-4* in *Arabidopsis*, *RMS1-5* in pea, *DAD1-3* in *Petunia hybrida* and *DWARF* (*D*) and *HIGH TILLERING DWARF* (*HTD*) in rice act in the same pathway with conservative function (Sorefan *et al.* 2003, Johnson *et al.* 2006, Zou *et al.* 2006, Arite *et al.* 2007, McSteen 2009; Table 1).

Further Johnson *et al.* (2006) and Zou *et al.* (2006) verified that recessive mutants of *MAX*, *RMS*, *DAD* and *D* exhibited a weakening inhibition of axillary buds and promoted branching. In fact, *MAX3, RMS5, DAD3* and *HTD1* were orthologous genes and encode carotenoid cleavage dioxygenase CCD7. *MAX4, RMS1, DAD1* and *D10* encode CCD8 (Sorefan *et al.* 2003, Snowden *et al.* 2005). Meanwhile, the recently discovered D27 (Lin *et al.* 2009), an iron containing protein with an enzymatic function, also acts as a new member participating in the biosynthesis of strigolactone. These enzymes cleave β-carotene into a mobile intermediate (Schwartz *et al.* 2004) that can be transported and further modified by cytochrome P_{450} (Booker *et al.* 2005). *MAX1* encodes P_{450} that could repress axillary buds growth *via* regulating flavonoid-dependent auxin retention in the buds and underlying stem (Lazar and Goodman 2006).

The genes described above act in the strigolactone(s) biosynthesis pathway. Compared with genes involved in biosynthesis, genes related with strigolactone(s) signaling were much more elusive. Recently found *d14* mutant (Arite *et al.* 2009) exhibits increased shoot branching and it is insensitive to exogenous strigolactone. In addition, Arite *et al.* (2009) demonstrated that *D14* functions either as a component of hormone signaling or as an enzyme that participates in the conversion of strigolactone to the bioactive form. However, the precise function of *D14* has not been annotated yet. MAX2, RMS4 and D3 are orthologous members of the F-box leucine-rich repeat (LRR) protein family (Stirnberg *et al.* 2002, Ishikawa *et al.* 2005), which probably act as a receptor for strigolactones and function in ubiquitin-mediated degradation of target proteins (Stirnberg *et al.* 2007). Coincidentally, *BRANCHED1* (*BRC1*) was found to be down-regulated in the *Arabidopsis max* mutants (Aguilar-Martinez *et al.* 2007) and upregulated in response to application of strigolactone (Masgugycuchi *et al.* 2009) and mutant *brc1*/*tb1* showed an increased branching phenotype (Aguilar-Martinez *et al.* 2007, Finlayson 2007). These facts suggested that the BRC1 might be the downstream target in the SMS pathway.

At the same time, experimental evidences suggested that there is a long-distance feedback signal in pea (*rms*), *Arabidopsis* (*max*) and rice (*d*) (Dun *et al.* 2009, Beveridge and Kyozuka 2010). The feedback signal shows two characteristics: one is up-regulation of the expression of the carotenoid cleavage *MAX/RMS/D* pathway biosynthetic genes, the other is severe reduction in the export of xylem-sap cytokinin from the roots. Reports indicated that the *RMS2* up-regulates *RMS1* and *RMS5* transcript abundance (Foo *et al.* 2005, Johnson *et al.* 2006) and down-regulate the xylem CK content (Foo *et al.* 2007) in pea. However, there was significant difference among species in the *RMS* up-regulation

Table 1. Genes involved in the synthesis or signaling pathway of strigolactone in different species

Protein	Rice	Maize	*Arabidopsis*	Pea	*Petunia*
Carotenoid cleavage dioxygenase 7 (CCD 7)	*HTD/D17*		*MAX3*	*RMS5*	
Carotenoid cleavage dioxygenase 8 (CCD 8)	*D10*		*MAX4*	*RMS1*	*DAD1*
Iron containing protein	*D27*				
Cytochrome P_{450}			*MAX1*		
F-box	*D3*		*MAX2*	*RMS4*	
Hydrolase (without annotation function)	*D14/D88/HTD2*				
TCP transcription factor	*FC1*	*TB1*	*BRC1*		

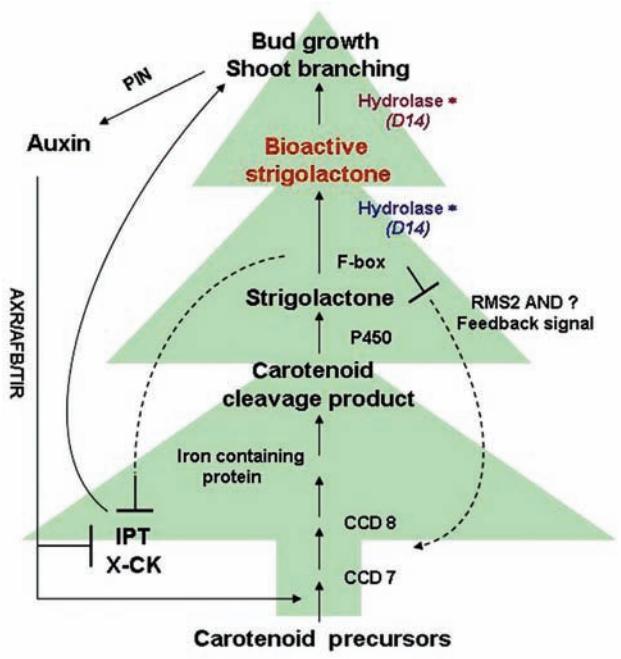

Fig. 1. Model for buds outgrowth and shoot branching *via* strigolactone and SMS/RMS pathway. Strigolactone, synthesized from carotenoids, is mediated by CCD7 and CCD8. Cytochrome P_{450}, F-box protein and α/β-fold hydrolase may be involved in the conversion of intermediate strigolactone to a bioactive strigolactone and subsequent signaling step. The signal moves upwards and is perceived in the shoot. Then it inhibits the buds growth and the shoot branching. Moving from shoot to root, the feedback signal partly depends on RMS2, enhances *CCD7* and *CCD8* expression and reduces X-CK export from the root. The identity of bioactive strigolactone remains unclear. This model is based on (Dun *et al.* 2009 and Beveridge and Kyozuka 2010).

magnitude, specifically, *RMS* signal transcripts in pea was substantially higher than that in rice and *Petunia* (Snowden *et al.* 2005, Arite *et al.* 2007, Umehara *et al.* 2008).

Meanwhile, researchers found that, it is part job of the feedback signal to enhance the level of auxin in the stem to several *MAX/RMS/D* pathway mutants (*max2/rms4*/*d3*) (Dun *et al.* 2009). In some ways, the transport capability of auxin in stem would also influence or be influenced by the SMS signal (Foo *et al.* 2005, Tanaka *et al.* 2006, Brewer *et al.* 2009).

According to the discussions above, strigolactone and the feedback signal maintain a homeostatic level of SMS (Beveridge 2006, Foo *et al.* 2007, Dun *et al.* 2009) (Fig. 1). The content of active strigolactone directly inhibits bud outgrowth and shoot branching (Ferguson and Beveridge 2009, Hayward *et al.* 2009).

Future issues

In fact, various factors are involved in the buds growth and the later shoot branching. These factors include the ontogenetic stage of the whole-plant (Stafstrom 1995), the particular node at which the bud arises, the age of the bud (Beveridge *et al.* 2003) and photoperiod (Horvath *et al.* 2003). Besides, in order to rationalize the findings from different studies on shoot-branching control, conclusions drawn from studies using *in vitro* or decapitated plants need to be testified by intact plants (Dun *et al.* 2006).

Environmental factors should be considered too. In the *rice*, strigolactone was involved in the absorption of minerals and had an indirect effect on branching as the branching increased when nutrients were rich and decreased when nutrients were limited (Umehara *et al.* 2008, McSteen 2009). In addition, *MAX2* was also involved in perception of red/far-red signals, which provided a mechanism to integrate light signals with branching (Shen *et al.* 2007).

More evidences need to elucidate the function of *D14* and its orthologs in *Arabidopsis* and pea during signal transduction of strigolactone, although Arite *et al.* (2009) showed that *D14* could function either as a signaling component for the perception or transduction of the hormonal signal or alternatively as the enzyme that catalyzes the metabolic conversion of strigolactones to the as yet unknown bioactive form.

Theoretically, stirgolactone regulates bud outgrowth and shoot branching *via* SMS and feedback signals. However, there are two point that need to be confirmed: one is to measure endogenous strigolactone content before/after auxin addition and depletion, the other is to make feedback signal clear in *Arabidopsis* and *Petunia*.

Two hypotheses were proposed to explain how strigolactone functions as a repressor of buds growth. One theory inferred that strigolactone directly moves into buds and inhibits the buds growth locally (Brewer *et al.* 2009). While the other suggested that strigolactone acts systemically by modulating auxin transport into buds and thus preventing buds activation (Crawford *et al.* 2010).

Perspective

Although we know little about the strigolactone biosynthesis, signal transduction pathways and receptor proteins, the discovery of this shoot branching inhibitor is a great breakthrough. It opens doors for the future research. Dun *et al.* (2009) said: "Having the strigolactone hormone in hand, we can test whether it affects cytokinin biosynthesis, metabolism or transports to buds". Further question is, whether strigolactone can act independently from auxin or not.

For all these fields, we need better understanding of the strigolactone biosynthesis and signal transduction pathways. Further, it is necessary to elucidate the way how strigolactone affects auxin or cytokinin biosynthesis, metabolism and transport and whether there are any other signals. Now we are on the road to reveal the mechanism of the branching.

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