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REVIEW PAPER

Shoot branching regulation and signaling

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Abstract
Plant development and structure are constantly adjusted throughout their life cycle to adapt environmental changes in nature. The amount of branches mainly depends on whether axillary buds form, release and growth of axillary buds. The plants branching is regulated by many factors including gene transcription, hormone homeostasis, and environmental factors such as light, water, and nutrition. People control shoot branching according to their demands to facilitate agricultural production. The activation and growth of lateral branches depend on a variety of internal and external environmental signals. Here we reviewed the recent progresses on genes, hormones, signaling materials, and external environmental conditions on the development of lateral branches in plant. Understanding these key nodes or regulatory networks is necessary and worthy challenges. The discussion of the factors affecting the formation of lateral branches provides a basis for the rational method of crop breeding and the cultivation of ideal plant type crops.

Keywords Environmental factor · Genes · Hormones · Shoot branching · Signaling

Introduction

Plant species harbor hundreds of thousands of appearances and structural features that help us to recognize and distinguish them. Most of the beautiful landscapes around us are made up of varied architecture of plants. These differences also provide favorable conditions for each plant to survive and reproduce in complex environments. An excellent example of a highly plastic development process is the control of shoot branching. Branching is one of the great inventions of plants (Jia et al. 2018; Xu et al. 2017). For the crop plants, shoot architecture is one of the most variable determinants of growth and productivity. In cereal crops, the vegetative growth stage of the shoot is called tiller. The number of tillers determine the number of flowers and seeds. The change of shoot architecture is caused by the variation in the number, length, height, position of shoots and the angle of branches (Barbier et al. 2019; Zhang et al. 2017). Axillary branch is the main branching system of angiosperms and gymnosperms, initiate laterally at a certain distance from the shoot apical meristem (Tian and Jiao 2015).

Axillary branches are related to phyllotaxis, which is the arrangement of leaves on the stem. The leaf can protect axillary meristem, which locates in the leaf axil (Long and Barton 2000). Axillary branch formation can be generally divided into three stages: axillary meristem initiation, meristem dormancy, and active meristem growth (Leyser 2003), whereas in some cases a bud may directly outgrow without a dormancy stage (Chen et al. 2019; Fu et al. 2014; Xu et al. 2016). For axillary meristem, there are two theories about its formation, i.e. the detached model and the de novo model. The detached model hypothesizes that axillary meristem directly derived from the shoot apical meristem cells, and these meristems never lost their characteristics of the meristem (Garrison 1955). Using live-imaging, it has been found that the formation of axillary meristem requires a group of meristem cells to continuously express meristem marker genes *SHOOT MERISTEMLESS* (*STM*). Then, *DORNRÖSCHEN* (*DRN*), *DORNRÖSCHEN-LIKE* (*DRNL*)

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and transcription factor REVOLUTA (REV) directly upregulated *STM* expression, causing axillary meristem (AM) to be activated. DRN/DRNL activation of *STM* expression depends on REV. DRN/DRNL and REV have cumulative expression patterns and protein interactions, which are essential for upregulation of *STM* expression. In addition, another REV-interaction protein, LITTLE ZIPPER3 disturbs the interaction of DRN/DRNL-REV to negatively regulate *STM* expression (Shi et al. 2016; Zhang et al. 2018). The origin of AMs depends on a sustained *STM* expression. Recent studies have shown that ARABIDOPSIS THALIANA HOMEOBOX GENE1 (ATH1) protein interacts with STM protein to form a self-activating circuit of *STM*. This helps to maintain the expression of the meristem marker gene (*STM*) in the leaf axils of Arabidopsis so that the fate of meristem cells can be maintained (Cao et al. 2020). In comparison, the de novo model suggests that axillary meristem begins to regenerate from leaf axillary cells which have lost stem cell identity and have differentiated to be leaf cells (Snow and Snow 1942). In histologically, axillary meristem origins appear to be different among different species. For example, there are distinct meristem cells at the base of each leaf in potato (Yamashita and Tahara 2006). However, obvious axillary meristem can be identified till after leaf formation during vegetative growth of Arabidopsis (Long and Barton 2000). Also, STM-expressing cell lineage clearly showed that axillary meristem derives from a meristematic cell population that never differentiated. Therefore, the detached model seems better to explain the axillary meristem initiation.

In Arabidopsis, the *CLAVATA* (*CLV*)-*WUSCHEL* (*WUS*) negative feedback loop coordinates stem cell proliferation with differentiation in the meristem, and its expression marks the end of the axillary bud formation alongside the establishment of a functional shoot apical meristem (Schoof et al. 2000). There are three forms of meristem dormancy, including paradormancy, ecodormancy, and endodormancy. Paradormancy is caused by endogenous signals from outside the bud, such as some plant hormones. Ecodormancy is caused by environmental influence on bud activity. Endodormancy, mainly in perennials, is a deeper state of bud inactivity that causes transforms in the internal state of the bud that cannot be changed by eliminating the factors that cause these changes (Lang et al. 1987). Thus, the final number of branches is determined by the amount of axillary meristems, the release of dormancy, and the activity of axillary buds.

Importantly, much of the plant's shape comes from the regulation of bud growth. In genetic analysis, it has been found that a few transcription factors encoding genes affect axillary meristem initiation. For example, *LATERAL SUPPRES-SOR* (*LS* or *LAS*) of tomato and Arabidopsis, encoding a GRAS domain protein, is most likely to be a transcription factor, and its homolog named *MONOCULM1* in rice has been identified as an axillary meristem initiation regulator (Greb et al. 2003; Li et al. 2003). After initiation, axillary meristems develop in the axil and then give rise to a secondary shoot from a bud that is initially dormant. The bud can be activated to grow into a secondary shoot.

There are many factors that affect the development of lateral branches, including the apical dominance, plant hormone, sugar, light, and the plant's own heredity. In this paper, we mainly review the recent advancement in the effects of genes, hormones, signaling materials and external environment conditions on the lateral development.

Genes that regulate shoot branching

R2R3 MYB-family Blind gene of tomato and its homologs *REGULATORS OF AXILLARY MERISTEMS1–3* (*RAX1–3*) in Arabidopsis participate in axillary meristem initiation (Müller et al. 2006). Beyond that, a *bHLH* family transcription factor *LAX PANICLE1* (*LAX1*) in rice, barren *stalk1* in maize, and *REGULATOR OF AXILLARY MERISTEM FORMATION* (*ROX*) in Arabidopsis, have also been identified to affect axillary meristem initiation (Gallavotti et al. 2004; Woods et al. 2011; Yang et al. 2012). *REV* encodes a class III homeodomain/leucine zipper TF (*HD-ZIPIII*), which has a broad expression pattern in many tissue types. *REV* mutants present defects in the development of the shoot apical meristem, leaves, vasculature, and roots. NAC domain proteins CUC2 and CUC3 have partially distinct functions in axillary meristem initiation. CUC2 slightly affects axillary meristem initiation, while CUC3 functions as a major regulator of axillary meristem initiation. Compared with single mutant, *las cuc3* double mutants showed more frequent axillary bud defects, indicating that *las* and *cuc3* have overlapping functions in Arabidopsis axillary meristem initiation (Yang and Jiao 2016). In barley (*Hordeum vulgare*), the *uniculm2* (*cul2*) mutant blocked the development of the axillary meristems and showed a lack of tillers developed from the crown (Okagaki et al. 2018). Li et al. (2003) used map-based cloning to isolate the *MOC1* gene controlling tiller growth in rice from extremely low-tillering mutants that occur naturally in rice. Further studies showed that the *MOC1* gene controlled the initiation of axillary meristems and the formation of tiller buds, as well as the ability to promote the elongation of tiller buds. In the leaf axils of the mutant, the axillary meristem lacked the *MOC1* gene, leading to the failure of the axillary meristem initiation and tiller buds formation, resulting in the extreme low-branching phenotype of rice. *MOC1* locates in the nucleus and regulates rice tiller by influencing downstream of *OsH1* (the initiation, establishment, and maintenance of meristem) and *OsTB1* (the lateral bud elongation). *OsH1* and *OsTB1* were significantly reduced in the *moc1* mutant and therefore *moc1*

may be the initiative gene for tiller control in rice. In maize, *TB1* is a key gene that controls branching. Although the teosinte is highly branched, domesticated maize has a single stem with male at the top and female at lateral ear. High expression of *TB1* increased the repression of branching in maize (Studer et al. 2011). *TB1* homolog named *OsTB1* or *FINECULM1* in rice and *BRANCHED1* in Arabidopsis, pea, and tomato have also been identified to participate in lateral development regulation (Braun et al. 2012). The *TB1/BRC1* gene encodes a TCP transcription factor and is specifically expressed in axillary buds. Overexpression of these genes represses lateral branch formation, whereas their loss-of-function mutations positively regulate it. This Blind/RAX pathway affects vegetative axillary meristem initiation of Arabidopsis and vegetative and reproductive branching of tomato (Yang et al. 2012; Müller et al. 2006). In Arabidopsis, *AtBRC1* and *AtBRC2* both negatively regulate the development of lateral branches, and *AtBRC1* plays a more important role than *AtBRC2*. *AtBRC1* gene mainly expressed during axillary bud development, and its expression was negatively correlated with the growth of buds. The mutant phenotype of *brc1* was non-pleiotropic, while the constitutive overexpression of *AtBRC1* reduced the growth of the whole plant. However, recent studies have shown that *AtBRC1* is not a necessary condition for inhibition of Arabidopsis buds (Seale et al. 2017). In addition, the *AtBRC1* homologous genes identified in tomato, pea and rose have been found to be involved in the inhibition of stem branching (Barbier et al.2015; Martín-Trillo et al. 2011; Braun et al. 2012). Two recessive of *ELIGULUM-A* (*ELI-A*) partially restored the tiller phenotype of *uniculm2* mutant. However, the *ELI-A* mutant plants were stunted and had fewer tillers. *ELI-A* is conserved in terrestrial plants, but the protein encoding is still unclear (Okagaki et al. 2018). *DOMAINS REARRANGED METHYLASE 2* (*OsDRM2*) which encodes DNA methyltransferases also regulates tillering in rice. The tiller number of *Osdrm2* mutant decreased significantly (Moritoh et al. 2012). The *Dad1/phCCD8* gene of petunia encodes dioxygenase. When the *Dad1/phCCD8* gene was absent in the plant, it was manifested as increased branching, shorter internode of the stem, and reduced root elongation. The *Dad1* gene was transferred into petunia mutant through the transgenic method, so that the phenotype of the mutant with high branching was changed, and the plant height was increased. The phenotype of the transgenic strains with restored mutation was no different from that of the wild type. Some petunia *dad1-1* mutants were grafted on wild-type rootstock as scions to restore the wild-type phenotype. Grafting experiments on petunia mutants showed that the root and stem could produce signaling molecules via long-distance to control the growth of axillary buds. Mutations of *dad1-1* have all the characteristics of CKs and auxin overexpression and gibberellin (GA) suppression, which may be the phenotype of increased branching caused by the interaction between the three hormones (Cai et al. 2018). Acquaintance results were also found in mutants of pea *RMS*, and further tests, based on the identification of *RMS1* and its predictive protein sequences, demonstrated the hypothesis that a branch inhibitor is a novel hormone-like substance (Sorefan et al. 2003).

Shoot branching regulation by hormones

Auxin

Auxin is produced by young growing leaves and travels to the stem through a specific polar auxin transport (PAT), thus contributing to bud growth (Bennett et al. 2016; Dong et al. 2013). Some researchers suggest that auxin from the main stem inhibits the growth of axillary buds by inhibiting and/or preventing the outflow of auxin from axillary buds (Balla et al. 2011, 2016; Sachs 1969). Several protein families are participated in active auxin transport, for instance the influx facilitators AUXIN INFLUX CARRIER PROTEIN 1 (AUX1)/LIKE-AUX1 (LAX) proteins, the p-glycoprotein auxin efflux carriers (PGP), and the PINFORMED auxin efflux carriers (PIN) (Paponov et al. 2005). *OsPIN1*, a polar auxin transporter, plays an important role in rice auxin-dependent tillers. *OsPIN1*-RNAi transgenic plants produced more tillers due to auxin-mediated axillary bud inhibition. The same phenotype was found in *OsPIN2*-overexpressed transgenic plants. Since *OsLazy1* was significantly down-regulated in transgenic rice, *OsPIN2* seems to regulate tillers by inhibiting *OsLazy1* (Parry et al. 2012). In the *pin-formed1* mutant and *aux1* mutant, the former affects an important auxin intracellular outflow transporter, while the latter shows impaired auxin inflow, the axillary auxin minimum disappears, and axillary meristems activation fails (Wang et al. 2014a, b). In Arabidopsis, *AUXIN-RESISTANCE1* (*AXR1*) further inhibits axillary bud formation. Auxin, the first hormone found involved in regulation of shoot branching, has been the focus of attention for more than 100 years (Ongaro and Leyser 2008). A pioneering research by Thimann and Skoog (1933) has shown that removal of the stem tip of broad beans (*Vicia faba*) stimulates axillary bud growth, and application of the plant hormone auxin to the stump of the severed plant significantly inhibits axillary bud growth. The experiment showed that the outflow of auxin in lateral bud promoted the growth of lateral shoot. The auxin in the whole plant stem is mainly derived from the terminal bud, while the auxin in the stem after capping is mainly derived from the lateral bud, and the auxin from the lateral bud can be inhibited by the external supplement of auxin from the terminal bud. However, in pea, strong inhibition of the specific exit of auxin from the bud did not prevent early

desquamate induced bud growth, but reduced bud growth after 2 days without affecting auxin transport in the main stem (Chabikwa et al. 2019). Taken together, these observations suggest that auxin output from axillary buds is not necessary to initiate bud growth, but is important for sustained bud growth. In rice, *OsIAA6*, which is preferentially expressed in axillary meristem at the base of the stem where tillers emerge, inhibited the growth of axillary buds and subsequent tillers. The tiller number of the *osiaa6* mutant is approximately two-fold compared to the wild type, as the axillary buds are released at elongated nodes, whereas in the wild type it is usually degraded. Therefore, *OsIAA6* seems to have an effect on axillary bud growth rather than axillary meristem formation, since only one axillary bud is developed at each node. Similarly, because *OsPIN1* and *OsTB1* are down-regulated in *osiaa6* mutant, *OsIAA6* regulates axillary bud growth and tiller by regulating auxin signaling (Jung et al. 2015). *YUCCA* encodes an enzyme similar to flavin monooxygenase that inhibits the growth of Arabidopsis axillary buds by increasing endogenous auxin levels. Conversely, in the *yucca1* mutant, the growth of most buds in the axils of rosette leaves was inhibited (Zhao et al. 2001).

Cytokinins

Although auxin released by the terminal bud plays a key role in formatting apical dominance, the inhibition of lateral branch growth is not caused by auxin released by the terminal bud directly into the lateral bud (Su et al. 2011; Cai et al. 2018; Cheng et al. 2013). Normal axillary meristem initiation requires CKs biosynthesis and signal transduction, evidenced as the mutations in CKs biosynthesis genes, CKs receptor genes, and downstream B-type *ARABIDOPSIS RESPONSE REGULATOR* (*B-ARR*) TF genes disrupt axillary meristem initiation (Müller et al. 2015; Wang et al. 2014b). Werner et al. (2001) reduced the contents of endogenous CKs through the overexpression of *CKX* in transgenic tobacco plants. Plants lacking CKs develop stunted buds with smaller apical meristem. Exogenous application of CKs can promote lateral growth and CK levels increase when buds are activated. Plants lacking CKs developed stunted buds with small apical meristem, the plasticizing time is prolonged, and leaf cell production is significantly lower than that of the wild type, indicating that CKs are absolute requirement for leaf growth (Werner et al. 2001). Studies have shown that CKs can be transported upward with xylem SAP into lateral buds and promote their growth, and treatment of lateral buds by exogenous cytokinins can break the apical dominance of plants (Davière and Achard 2017). At the same time, the increased level of CKs in axillary buds is closely related to the accelerated growth rate (Shimizu-Sato and Mori 2002). Isoamyl transferase (IPT) controls a rate-limiting step in CKs biosynthesis and transcription level of IPT gene was regulated by auxin level (Li et al. 2018). Suppression of CKs biosynthetic genes synthesized by auxin is well known. Under the condition of removing the apex dominance, the expression of two pea genes *PsIPT1* and *PsIPT2* was rapidly up-regulated and CKs content increased. However, CKs biosynthesis was first increased in node tissue rather than in axillary bud. Parts of the stem CKs are transported to dormant buds to stimulate their growth (Miyawaki et al. 2004; Nordstrom et al. 2004; Tanaka et al. 2006). Rice CKs oxidase (OsCKX2) is an enzyme that degrades CKs and controls axillary bud growth and tiller by inhibiting CKs accumulation in buds. Compared with WT, *OsCKX2*-RNAi plants had more tillers, while *OsCKX2*-OE transgenic plants had fewer tillers (Yeh et al. 2015). Three different types of CKs are produced in higher plants, including isopentenyladenine (iPT), zeatin (Z), and dihydrozeatin (DZ). Müller et al. (2015) demonstrated that CKs synthesis and signal mutants of Arabidopsis were related to the stem and branches of intact plants, but not to the severed plants. This suggests that the role of CKs is to promote (in intact plants) escape from apical dominance, not to promote the growth of decapitated induced buds. In rice and pea, CKs down-regulate the expression of the *FINE CULM1/PsBRANCHED1* (*FC1/PsBRC1*) gene, a negative regulator of lateral branch. However, in pea, CKs also appear to be independent of *PsBRC1*, since *PsBRC1* mutants respond to CKs applications (Braun et al. 2012; Minakuchi et al. 2010). CKs have also recently been proposed to regulate bud growth by controlling auxin transport. In Arabidopsis, CKs promote the polarization of auxin efflux carriers, while CKs signal deletion mutant branches decrease, the result from the decrease of efflux carriers polarization (Waldie and Leyser, 2018).

Strigolactones

SLs, known as carotenoid signals, exude from the root and move toward the apex, inhibiting axillary branches (Umehara et al. 2008). Genes involved in SLs biosynthesis or signaling play an important role in controlling axillary bud growth and SLs-mediated branching, such as an *iron-binding protein D27,* the *carotenoid cleavage dioxygenases 7* and *8,* a *cytochrome P450 protein MAX1* and *DWARF 14* (Yang et al. 2019; Zhao et al. 2020). *DWARF 27 (D27)* encodings a new iron-containing chloroplast protein, which is mainly expressed in young leaves, axillary buds, inflorescence primordium, lateral roots, and crown roots. Exogenous addition of GR24 can significantly inhibit the growth and tiller of axillary buds in *d27* mutant. These data indicate that *D27* regulates the growth and tiller of axillary buds and participates in the synthesis of SLs (Lin et al. 2009). *DWARF3*, an Arabidopsis *MAX2* homolog that encodes a nuclear-localized F-box protein, functions in forming SCF complex and interacting with *DWARF 14* and *DWARF 53* to inhibit

the germination and tiller of axillary buds in rice. Rice *OsMAX1a* and *OsMAX1e* are homologous genes of Arabidopsis *AtMAX1*, which regulate the synthesis of SLs and thus inhibit branch growth. The tiller number of *OsMAX1a*-RNAi and *OsMAX1e*-RNAi plants was 40% higher than that of untransformed WT (Wai and An 2017). In addition, SLs can negatively regulate the transport of auxin from the main stem and restrict its movement from the axillary bud to the stem (Crawford et al. 2010; Domagalska and Leyser 2011). Another view is that SLs are the secondary messengers of auxin, which directly inhibit the growth of buds (Ferguson and Beveridge 2009). So these are the two models of how SLs and auxin interact to regulate branch branching based on different experimental systems. Compared with the WT, in *DWARF10*-RNAi transgenic plants, due to the reduced expression of most *OsPINs* in the stem nodes, the auxin transport capacity was reduced, the auxin content in the stem tip was high, and the tiller number was reduced (Arite et al. 2007). Zhang et al. (2010) found that the application of exogenous auxin significantly increased the expression of *DWARF10* in stem nodes, and exogenous CKs inhibited the expression of *DWARF10*. *DWARF10* plays a key role in controlling axillary bud growth and tiller by reducing auxin level and promoting CKs biosynthesis. *Dwarf14* is a novel esterase gene involved in SLs signaling, which controls axillary bud growth and tiller in rice. Although *d14* mutants were similar to WT in that there was only one axillary bud per leaf axil, the axillary bud germination of *d14* mutants was earlier than that of WT (Gao et al. 2009).

Other hormones

Recent studies suggest that brassinosteroids (BRs) regulate the expression of boundary-specific genes in organs and contribute to the formation of boundaries (Gendron et al. 2012; Xu et al. 2014). At the same time, BRs are also involved in controlling the formation of branching plants. *DWARF AND LOW-TILLERING* (*DLT*) participates in feedback inhibition of BR biosynthesis, and rice *dlt* mutation showed reduced branching phenotype. Overexpression of *GSK3/SHAGGY-like kinase* (*GSK2*) altered BR signaling and reduced tiller number (Tong et al. 2012). In contrast, *bri1-EMS-suppressor 1* (*BES1*) is a positive regulator of BR signaling, and the functional mutant of Arabidopsis *BES* showed more branching phenotypes than RNAi strains (Wang et al. 2013; Yin et al. 2002). GAs usually inhibits stem branching, while plants that overexpress the GA catabolism gene and GA-deficient mutants exhibit more branching phenotypes. GA biosynthetic mutant *ga1-3* in Arabidopsis and overexpression of *AtGA2ox1* in *Paspalum notatum* also lead to very low levels of endogenous active GA, which increase the number of vegetative tillers (Agharkar et al. 2007). In general, although different hormones cause plant phenotypic acquaintance, hormones play different roles. For example, both SLs and GA will repress tiller buds growing, but GA treatment promotes stem growth and inhibits tiller growth, while SLs treatment does not promote stem elongation (Nakamura et al. 2013). ABA signaling responses in Arabidopsis *brc1* mutants were significantly lower than those in the wild type (González-Grandío et al. 2013; Wang et al. 2016). González-Grandío and Cubas (2014) demonstrated the role of ABA in *BRC1* downstream, because *BRC1* induced reaction of two key regulatory factors of ABA, *ABRE-BINDING FACTOR 3* (*ABF3*) and *ABA INSENSITIVE 5* (*ABI5*). It was also found that *BRC1* binds and positively regulates three transcription factors: HOMEOBOX protein 21 (HB21), HOMEOBOX protein 40 (HB40), and HOMEOBOX protein 53 (HB53). These three proteins, together with BRC1, enhance the expression of *9-cis-epoxycarotene dioxidase 3* (*NCED3*), which is the main enzyme in ABA biosynthesis and leads to ABA accumulation in buds (González-Grandío et al. 2017). This finding demonstrated a direct relationship between BRC1 and ABA signaling and placed ABA downstream of BRC1. Consistent with this, *BRC1* expression was found to be insensitive to ABA application (Yao and Scott 2015).

Shoot branching regulation by external environment

Light

In many species, low light intensity and low red/far-red ratio (R/FR) negatively regulate shoot branching (Kebrom et al. 2006). The signaling function of light in plant branches was first discovered by Kebrom et al. (2006), in which they proposed that activation of PHYB inhibited the expression of sorghum *SbTB1* gene, resulting in high branch height (Kebrom et al. 2006). Similarly, in Arabidopsis, low R/FR ratio was found to favor up-regulation of *AtBRC1* by PHYB pathway, which is necessary to reduce bud branching (González-Grandío et al. 2013). Correspondingly, *AtBRC1* was rapidly and locally down-regulated after increasing R/FR ratio (Holalu and Finlayson 2017). In addition, the rose exposed to the dark had no buds and higher *RhBRC1* transcription levels than the plants exposed to light (Roman et al. 2016). These results indicate that *BRC1* expression is very sensitive to light. However, this regulation may involve different mechanisms (Kebrom et al. 2010).

Nutrient elements

In Arabidopsis, de Jong et al. (2019) found that the extent to which some Arabidopsis species branch is influenced by nitrogen content. The study used two different Arabidopsis

strains to describe changes in bud branching with nitrate supply. The results showed that highly malleable lines were associated with extreme branching phenotypes, with the most branching lines under high nitrate conditions and the least branching lines under nitrate absence. *OsmiR393* is related to rice tillering enhanced by nitrogen. *OsmiR393* was significantly expressed in axillary meristem, and the axillary buds of OE transgenic plants grew vigorously and tillers increased. This gene regulates auxin signal transduction in axillary buds when up-regulation of its expression in nitrogen fertilizer treatment (Li et al. 2016; Xia et al. 2012). Soil nitrate can promote the synthesis of CKs and the growth of axillary buds. However, auxin can negatively regulate *ADENYLATE ISOPENTENYLTRANSFERASE* family members, inhibiting synthesis of CKs to antagonise the influence of nitrate (Nordstrom et al. 2004). In rice, nitrogen increased CKs by increasing the expression level of *OsIPTs* in nodes. In addition, three hours after ammonium nitrate treatment, the expression of genes related to SL synthesis in roots and nodes was down-regulated, indicating that the inhibition of nitrogen on SL synthesis occurred at least partially through the CKs pathway (Xu et al. 2015). Li et al. (2016) showed that the high uptake of ammonium nitrate in the root environment inhibited the expression of auxin synthesis and signal transduction related genes (*OsTIR1, OsAFB2,* and *OsIAA6*) and *OsTB1* through inducing the overexpression of *miRNA393* in the buds, which reduced the sensitivity of axillary buds to auxin and thus promoted rice tillering. In addition to its nutritional role, asparagine is also a signal of plant nitrogen status, which can counteract the expression of *BRC1* by stimulating CKs. In rose bushes, asparagine is the main nitrogen element during bud growth. Sucrose, glucose, and fructose must combine with asparagine to up-regulate the expression of *IPT3* gene near stem and bud, so as to promote bud growth (Le Moigne et al. 2018). In wheat, phosphorus deficiency directly changed the law of normal tiller emergence by reducing the rate of tiller emergence (Rodríguez et al. 1999) Low phosphorus growth conditions have increased the content of SL in many species, while low levels of inorganic phosphate have decreased CKs yield, all of which lead to inhibition of branch branching (Rodríguez et al. 1999; Yamada et al. 2014). In the absence of phosphorus, plants regulate branching by affecting the expression of *OsMAX1a* and *OsMAX1e* genes (Wai and An 2017). Polyamines, fatty nitrogen compounds, also play an important role in controlling axillary bud development and bud growth in plants. Breaking down the expression of the *Sadenosylmethionine decarboxylase* (*SAMDC*) gene in Arabidopsis results in high levels of putrescine and low levels of spermidine and spermine. Because of the change of polyamine homeostasis in plants, the dormancy of axillary bud was broken and more branching phenotypes were observed (Ge et al. 2006).

Shoot branching regulation by signal transducers

Sugars are known to promote bud growth in many species (Tarancón et al. 2017; Ferreira et al. 2018). Sugar is not only a source of carbon for plant metabolism, but also an important signaling agent that affects many developmental processes, including *BRC1* gene expression (Sakr et al. 2018; Barbier et al. 2015; Dong et al. 2019; Ma et al. 2017). Mason et al. (2014) demonstrated that the initial signal released by decapitation in pea was an increase in the availability of sugar, rather than a decrease in apical auxin as traditionally believed. In addition, they also reported that the time when the sugar flux inside and outside the bud increased closely related to the down-regulation of *BRC1* expression. In this process, sugar is more likely to act as a signaling agent, since many non-metabolizable sugar analogens can trigger germination and inhibit *BRC1* expression. In addition, this effect of sugar on *BRC1* transcription may directly or indirectly regulate CKs biosynthesis and SLs signal transduction through sugar (Barbier et al. 2015; Rabot et al. 2012).

In plant growth regulator, nitric oxide (NO) is a gaseous lipid free radicals, as one can be a variety of hormone signaling molecules induced by fast, through the role of second messenger to assist complete plant growth hormone signal regulation, including promote seed germination, inhibition of taproot and hypocotyl elongation, induced lateral root and adventitious root and root hair, the control of cell polarity form, involved in plant geotropism morphogenesis etc., in the plant by more and more attention in the body (Sanz et al. 2015; Wen et al. 2016). NO can directly regulate the physiological processes of many plants by regulating post-transcriptional modifications of genes (Ni et al. 2017; Gong et al. 2019; Yan et al. 2019). For example, in the auxin signaling pathway, NO and auxin regulate plant growth and development through S-nitrosylation. S-nitrosylation TIR1 can enhance the interaction between TIR1/AFB and Aux/IAA, leading to accelerated degradation of Aux/IAA and regulation of auxin signal (Zhang et al. 2019). NO also regulates the assembly of SCFTIR1/AFB1 E3 ubiquitin ligase complexes in Arabidopsis through S-nitrosylation regulation, thereby affecting the activation of auxin signaling (Iglesias et al. 2018). In recent years, it has been found that the NO signaling pathway inhibits the internal and polar auxin transport of the exocrine auxin transporter PIN-formed (PIN) (Ni et al. 2017). Zhang et al. (2019) found that in *GSNOR1* functionally deficient mutant *gsnor1–3*, plants showed a high level of SNO content, and *PIN2* expression was destroyed in the root of the mutant, thereby affecting auxin signal conduction and polar auxin transport.

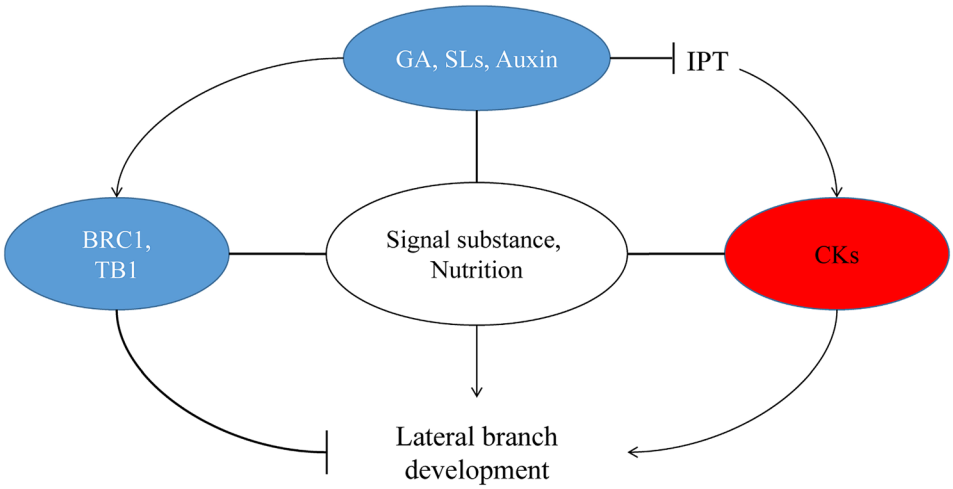

Fig. 1 A model diagram of the effect of various hormones and genes on the development of lateral branch development

Interestingly, Terrile et al. (2012) and Shi et al. (2015) put forward the inconsistent views that S-nitrosylation inhibited Aux/IAA degradation to inhibit auxin signaling, and disrupted auxin polar transport by reducing the level of *PIN*. A more accurate explanation requires further research. H_2O_2 plays an important role in the regulation of the growth and development of lateral branches (Liu et al. 2010). After exogenous spraying 5 mM H_2O_2, the apex dominance of plants was enhanced and the growth of lateral buds was inhibited. The study found that after the silencing of NADPH oxidase coding gene (*RBOH1* and *WF11*) of tomato, the H_2O_2 content in the plant significantly decreased, and the growth of lateral shoots was significantly promoted, reducing the apical advantage of the plant. The reason why H_2O_2 is involved in regulating the growth and development of lateral shoot of tomato is that H_2O_2 can directly affect the synthesis of auxin, and the expression changes of *IPT2* and SL synthesis genes (*CCD7, CCD8,* and *MAX1*) in stem and root are also related to H_2O_2 (Chen et al. 2016).

Conclusion

In conclusion, we can see that shoot branching is affected by many factors, among which the relevant genes, hormones, signaling materials, and external environment play key roles in this progress (Fig. 1). These factors may work individually or together, contributing to the establishment of plant architecture. However, there is a long distance to completely figure out the control or regulation of development of lateral branches. Although many genes have been identified in the regulatory branches recently, their upstream regulators and downstream targets are largely unknown. Branching is a phenotype controlled by multiple genes, but the relationship between genes is also poorly understood. The branch phenotypes of many mutant plants are familiar with plant hormone response phenotypes and changes in plant hormone content have been detected, but it is not clear that genes are the intermediate link that affects plant hormones. Fundamental understanding of these aspects will aid in controlling plant branches to meet the diverse requirements for practical production.

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