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Update

The molecular and genetic regulation of shoot branching

Zhiwei Luo [1,2], Bart J. Janssen [1] and Kimberley C. Snowden [1,*,†]

1 The New Zealand Institute for Plant and Food Research Limited, Auckland 1025, New Zealand
2 School of Biological Sciences, University of Auckland, Auckland 1010, New Zealand

*Author for communication: kimberley.snowden@plantandfood.co.nz
†Senior author.

Z.L. and K.C.S. conceived the structure and content, and prepared the figures; all authors contributed to the writing. K.C.S. agrees to serve as the author responsible for contact and ensures communication.

The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plphys/pages/general-instructions) is: Kimberley C. Snowden (kimberley.snowden@plantandfood.co.nz)

Abstract

The architecture of flowering plants exhibits both phenotypic diversity and plasticity, determined, in part, by the number and activity of axillary meristems and, in part, by the growth characteristics of the branches that develop from the axillary buds. The plasticity of shoot branching results from a combination of various intrinsic and genetic elements, such as number and position of nodes and type of growth phase, as well as environmental signals such as nutrient availability, light characteristics, and temperature (Napoli et al., 1998; Bennett and Leyser, 2006; Janssen et al., 2014; Teichmann and Muhr, 2015; Ueda and Yanagisawa, 2019). Axillary meristem initiation and axillary bud outgrowth are controlled by a complex and interconnected regulatory network. Although many of the genes and hormones that modulate branching patterns have been discovered and characterized through genetic and biochemical studies, there are still many gaps in our understanding of the control mechanisms at play. In this review, we will summarize our current knowledge of the control of axillary meristem initiation and outgrowth into a branch.

Axillary meristem initiation

The axillary meristem is initiated from the boundary between the shoot apex and leaf primordia

Axillary meristem initiation occurs in the meristematic cell niche at the adaxial side of the leaf axils and requires the establishment of a boundary between the main shoot and the leaf primordium. Boundary formation is critical for plant organogenesis, separating the pluripotent meristematic cell population that remains indeterminate from the developing organs. The cells in boundaries have reduced cell division, down-regulated cell-cycle-related genes, and relatively stiff cell walls (reviewed in Wang et al., 2016; Richardson and Hake 2019). In addition to physically separating neighboring tissues, boundaries contribute to various developmental processes, including axillary meristem initiation, leaf shape, fruit dehiscence, and organ abscission (reviewed in (Hepworth and Pautot, 2015)). The low rate of cell division within the boundary is controlled by a regulatory network in which regulatory genes such as *CUC* (*CUP-SHAPED COTYLEDON*), *STM* (*SHOOT MERISTEMLESS*), and *LOB* (*LATERAL ORGAN BOUNDARIES*) suppress cell division and differentiation and modulate the spatial distribution of growth promoting hormones, such as auxin, gibberellin (GA), and brassinosteroids (BR; Jasinski et al., 2005; Borghi et al., 2007; Takeda et al., 2011; Bell et al., 2012; Wang et al., 2016; Richardson and Hake, 2019). Several studies

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- Recent work has shown that axillary meristem initiation and outgrowth is controlled by a complex network involving interactions between multiple hormones, miRNAs and transcription factors that integrate environmental information to optimize growth.
- BRC1 is a key hub protein that is involved in the control of branching. However, there is also BRC1 independent regulation of branching involving SL, auxin, CK, and T6P.
- The SL signaling repressors SMXL6,7,8 can act as TFs, and SMXL6 is able to bind directly to the SMXL6,7,8 and BRC1 promoters to suppress their expression.
- Both photosynthetic and signaling sugars have been increasingly recognized as important regulators of branching.

indicate that the boundary-expressed genes described above are required for axillary meristem formation, with loss-of-function or down-regulation of these genes resulting in organ fusion and axillary meristem defects, while overexpression of these genes led to ectopic axillary meristem formation (Greb et al., 2003; Vroemen et al., 2003; Hibara et al., 2006; Gómez-Mena and Sablowski, 2008; Raman et al., 2008; Lee et al., 2009; Spinelli et al., 2011).

Organ boundary and meristem identity genes form linked regulatory networks for axillary meristem initiation

The maintenance of meristematic competence and subsequent axillary meristem initiation is regulated by a set of transcription factors (TFs), which appear to be conserved between species. Some of these TFs are important for multiple developmental processes; however, in this section, particular attention is given to their roles in axillary meristem initiation (Figure 1). Axillary meristem initiation involves protein movements, transcriptional regulation, protein–protein interactions, and feedback regulation in multiple pathways. Such complexity can be illustrated by the regulation of STM, a meristematic marker, by at least two interconnected yet independent pathways, while at the same time reporting recent data on the wider network.

STM, like its homologs from other species (*ORYZA SATIVA HOMEOBOX1* (*OSH1*) in rice (*Oryza sativa*) and *knotted1* (*kn1*) in maize, *Zea mays*), is required for establishing and maintaining apical meristems as well as axillary meristem identity (Long et al., 1996; Shi et al., 2016). *STM* expression changes coinciding with axillary meristem initiation and is controlled by a number of regulators (Greb et al., 2003; Bolduc et al., 2012; Shi et al., 2016; Wang et al., 2017; Scofield et al., 2018; Zhang et al., 2018; Cao et al., 2020; Xue et al., 2020). Initially, *STM* expression in the leaf axils is low yet appears to be sufficient to maintain meristematic cell competence (Shi et al., 2016; Zhang et al., 2018; Cao et al., 2020). An ATH1 (ARABIDOPSIS THALIANA HOMEOBOX GENE1)-STM heterodimer can bind to the *STM* gene and maintain its expression (Cao et al., 2020). In addition, REVOLUTA (REV) can interact with DORNRÖSCHEN (DRN)/DORNRÖSCHEN-LIKE (DRNL) to promote *STM* expression. Early in development, LITTLE ZIPPER3 (ZPR3) prevents the interaction of REV-DRN/DRNL, resulting in low levels of STM. Later in development, ZPR3 expression is decreased allowing REV-DRN/DRNL to interact, promoting *STM* expression (Shi et al., 2016; Zhang et al., 2018).

STM can promote axillary meristem initiation by upregulating the expression of cytokinin (CK) biosynthesis genes (e.g. *ISOPENTENYLTRANSFERASE7* (*IPT7*)) and CK-response regulators (Jasinski 2005; Yanai et al., 2005). After STM-induced meristematic activity, activation of *WUSCHEL* (*WUS*) by CK signaling promotes axillary meristem initiation in the leaf axils (Shi et al., 2016; Wang et al., 2017). Interestingly, a recent study showed that WUS proteins are able to activate *STM* expression and bind to STM protein directly to promote *CLAVATA3* (*CLV3*) expression (Su et al., 2020). These results suggest that STM plays a crucial role in maintaining the shoot–leaf boundary during axillary meristem initiation and regulating hormone content during axillary meristem initiation.

LATERAL SUPPRESSOR (*LAS*) of *Arabidopsis thaliana* and its homologs, *Ls* of tomato (*Solanum lycopersicum*), *MONOCULM 1* (*MOC1*) of rice, *ERAMOSA* (*ERA*) of snapdragon (*Antirrhinum majus*), and *AaLAS* of *Arabis alpina* are boundary-specific GRAS family TFs that control meristem initiation through regulation of *STM* (Schumacher et al., 1999; Otsuga et al., 2001; Greb et al., 2003; Li et al., 2003; Mizzotti et al., 2017; Ponraj and Theres, 2020). *LAS* regulates *STM* expression through *REV*; however, mutation of *LAS* affects vegetative axillary meristems, while mutation of *STM* affects both shoot and floral meristem function (Endrizzi et al., 1996; Greb et al., 2003; Shi et al., 2016). Rice *moc1* mutants affect the expression of *OSH1* and *OsTB1* (a homolog of maize *teosinte branched1* (*tb1*)) in leaf axils only, whereas the overexpression of *MOC1* in rice resulted in tiller outgrowth from higher order tiller buds (Li et al., 2003), implying that *MOC1* may be a key regulator for both axillary meristem initiation and outgrowth.

Although the *LAS* function was conserved between perennial *A. alpina* and annual Arabidopsis and tomato (Ponraj and Theres, 2020), legumes appear to have lost a LAS-like TF during evolution (Mizzotti et al., 2017). The regulatory mechanism of *MOC1* in rice has been studied in some detail: Lin et al. (2012) and Xu et al. (2012) both reported that the anaphase promoting complex/cyclosome (APC/C) E3 ubiquitin ligase complex mediates the degradation of MOC1 in leaf axils, resulting in down-regulation of *OSH1* and repression of axillary meristem initiation. Xu et al. (2012) also showed that MOC1 degradation is cell-cycle dependent;

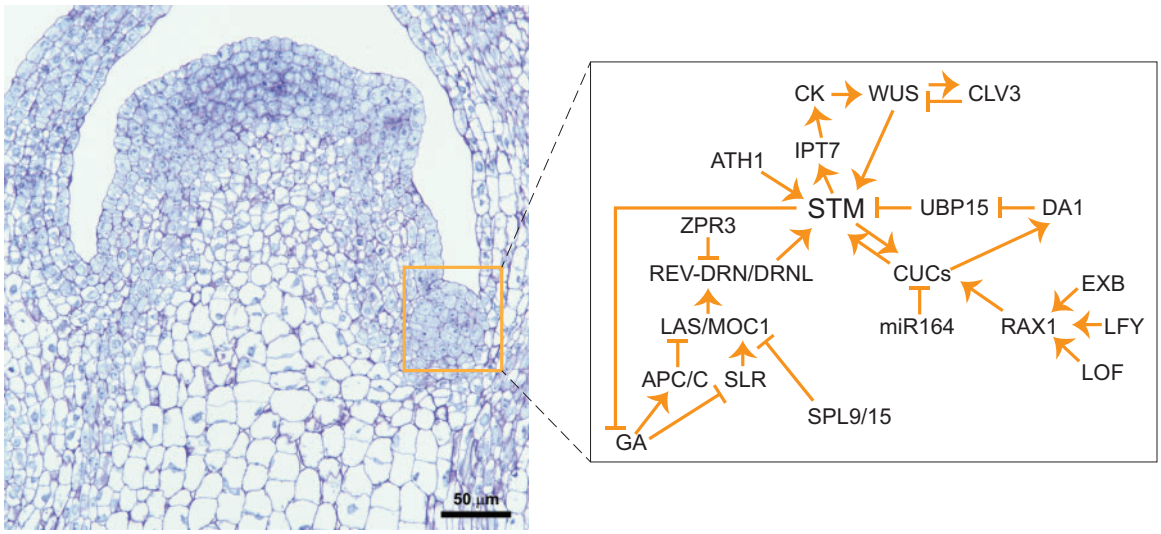

Figure 1 Interacting regulatory pathways for axillary meristem initiation at the boundary between shoot and leaf primordium. The photograph shows a longitudinal section of a petunia SAM and leaf primordium (scale bar is 50 μm). The inserted box denotes the region where the axillary meristem initiates. The expanded box shows the proposed regulatory networks. STM, a meristematic marker, promotes axillary meristem initiation through CK and the WUS-CLVs pathway. STM is regulated by both LAS/MOC1 through the REV-DRN/DRNL pathway and RAXs through CUCs and/or the DA1 pathway. These two pathways are interconnected by CUCs. LAS is degraded by the APC/C complex that involves GA signaling, while RAX1 is able to interact with a number of TFs such as EXB, LFY, and LOF. The arrows and blunt lines represent positive and negative regulation, respectively.

when the degradation was blocked, the accumulation of MOC1 resulted in an increase in tiller numbers. Based on these results, it is possible that the APC/C–MOC1 complex activates during the G1-phase to maintain MOC1 at a relatively low level in axillary buds (Xu et al., 2012); however, whether MOC1 directly regulates cell division is still unclear and whether *OSH1* or *OsTB1* are the transcriptional targets of MOC1 is yet to be confirmed. Liao et al. (2019) have shown that the DELLA protein SLENDER RICE 1 can prevent the degradation of MOC1. High levels of GAs are also able to activate the APC/C complex and promote degradation of MOC1 (Lin et al., 2020).

In Arabidopsis, a number of TFs have been shown to affect *LAS* expression, such as SQUAMOSA PROMOTER-BINDING PROTEIN-LIKE9 (SPL9) and SPL15 and CUC2 (Tian et al., 2014). Although evidence suggests that CUC2 proteins and probably CUC1 bind to the *LAS* promoter to enhance the expression of *LAS* (Hibara et al., 2006; Tian et al., 2014), an additive effect of axillary meristem defects was found in *cuc2 las* and *cuc3 las* double mutants (Hibara et al., 2006), suggesting LAS works at least partially independently of CUC2/CUC3. These lines of evidence suggest that LAS/MOC1 is a major regulator that integrates a number of signals and contributes to the STM-WUS axillary meristem initiation mechanism.

Studies of double mutants of *LAS* and *REGULATOR OF AXILLARY MERISTEMS1* (*RAX1*)/*Blind* reveal additional complexities in the regulation of axillary meristems through STM involving *RAX*, *CUCs*, and *microRNA164* (*miR164*; Schmitz et al., 2002; Müller et al., 2006). In the Arabidopsis *rax1 rax2 rax3* triple mutant, almost no axillary meristems were able to initiate and the *STM* mRNA was undetectable in the leaf axils, while the expression of *STM* in the shoot apical meristem (SAM) was unaffected (Müller et al., 2006). The axillary meristem defect in the *rax* mutants could be restored by exogenous application of CK or overproduction of CK in leaf axils (Wang et al., 2014). The expression of *RAX* genes is regulated by a number of TFs, such as EXB1 (EXCESSIVE BRANCHES, Guo et al., 2015), LFY (LEAFY, Chahtane et al., 2013), and LOF1 (LATERAL ORGAN FUSION1, Lee et al., 2009). *RAXs* modulate the expression of *CUC2* (Keller et al., 2006), which, as mentioned above, promotes *LAS* expression.

CUC1 and *STM* regulate each other's expression through a positive feedback loop, which also involves *miR164* (Raman et al., 2008; Spinelli et al., 2011; Scofield et al., 2018). This interaction requires the movement of STM protein from the SAM to the boundary, as a nonmobile version of STM failed to rescue the *stm* mutant and caused down-regulation of *CUC1–CUC3* expression in inflorescence meristems, resulting in phenotypes similar to those in the *cuc2 cuc3* double mutant (Balkunde et al., 2017). Recently, Li et al. (2020) found that CUC2 and CUC3 proteins also regulate the expression of *DA1* and the DA1 substrate UBIQUITIN-SPECIFIC PROTEASE15 (UBP15). When *DA1* is mutated, *STM* expression is lost and axillary meristems fail to initiate in Arabidopsis (Li et al., 2020), although a direct link between UBP15 or DA1 and STM has yet to be identified.

Axillary meristem outgrowth

Bud outgrowth from axillary meristems leads to the development of branches and is triggered by the perception of

developmental and environmental cues, such as meristem age and location, nutrients, light, and temperature (Janssen et al., 2014). The decision to grow into a branch also takes into account information from throughout the plant, such as the presence of additional growing shoots. Both internal and external factors are integrated to determine where and when a bud will grow to form a branch. Much of our current knowledge of the control of branch growth centers on the roles of plant hormones, particularly of auxin, CK, and strigolactones (SL; for in-depth reviews of the roles of auxin and CK in particular, see Muller and Leyser, 2011; Harrison, 2017; Barbier et al., 2019). Here, we will summarize advances that help clarify the role of SLs in branching, along with key recent results for other plant hormones.

SL is a core component of signaling and regulatory networks for branching

SL biosynthesis genes, such as *CAROTENOID CLEAVAGE DIOXYGENASE7* (*CCD7*), *CCD8*, and *MORE AXILLARY GROWTH1* (*MAX1*), and signaling perception genes, such as *DECREASED APICAL DOMINANCE* (*DAD2*)/*DWARF14* (*D14*)/*AtD14*/*RAMOSUS3* (*RMS3*) and *MAX2*/*D3*/*RMS4*/*PhMAX2A*, have been identified mainly through analysis of highly branched mutants from a number of model species (Beveridge et al., 1994, 1997, 2000; Booker et al., 2005; Snowden et al., 2005; Zou et al., 2006; Arite et al., 2007; Simons et al., 2007; Stirnberg et al., 2007; Arite et al., 2009; Xie et al., 2010; Hamiaux et al., 2012; Janssen and Snowden, 2012; Jiang et al., 2013). For axillary buds on these plants, reduced or abolished SL production or signaling resulted in alteration of their outgrowth potential from dormant to active growth, for instance, petunia (*Petunia hybrida*) *dad1* mutant plants produced branches at the leaf axils of the cotyledons and the first two basal nodes, where normally no branches develop in wild-type (WT; Snowden et al., 2005). The highly branched phenotype of SL-deficient mutants can be rescued by treatment with a synthetic SL analogue, GR24, or by grafting the mutant scion onto WT rootstocks, whereas these treatments cannot rescue the branched phenotype from the SL-insensitive mutants (Foo et al., 2001; Sorefan et al., 2003; Simons et al., 2007; Arite et al., 2009; Lin et al., 2009; Hamiaux et al., 2012; Waters et al., 2012). *CCD7* and *CCD8* have also been isolated in some woody perennial plants, such as poplar, kiwifruit, apple, and grape, and evidence suggests they have comparable roles to those observed in model systems, particularly in regulating branching in the shoot (Ledger et al., 2010; Vogel et al., 2010; Kohlen et al., 2012; Muhr et al., 2016; Pan et al., 2016; Foster et al., 2017; Gao et al., 2018; Wu et al., 2019; Ren et al., 2020). Collectively, these studies reveal a conserved function and regulatory pathway of SL signaling in controlling axillary bud outgrowth (Delaux et al., 2012; Ruyter-Spira et al., 2013; Janssen et al., 2014; Machin et al., 2019; Walker et al., 2019).

Grafting studies using SL mutants and corresponding WT plants from several species suggest that SL made in either the root or stem of plants can influence branching in the shoot system, and that SL moves acropetally through the plant. The mechanism of SL transport from the root to the shoot and into axillary buds is not completely resolved. Currently, PLEIOTROPIC DRUG RESISTANCE1 (PDR1) from petunia is the only characterized SL transporter, and *pdr1* mutants have reduced SL exudation from roots and produce more branches with vigorous outgrowth (Kretzschmar et al., 2012). PDR1 appears to be involved in local short-distance transport, such as unloading SLs from roots into soil and from the shoot into axillary buds (Sasse et al., 2015; Shiratake et al., 2019). PDR1 might also contribute to the long-distance root-to-shoot transport of SL; however, grafting experiments indicate that there must also be a PDR1 independent pathway, which might involve the vasculature and/or other transporters that target SL precursors (Sasse et al., 2015; Shiratake et al., 2019). It is unclear whether SL is transported through the xylem (Kohlen et al., 2011; Xie et al., 2015). Xie et al. (2015) could not detect SLs or carlactone, an SL precursor, from xylem sap of Arabidopsis, rice, tomato, cucumber (*Cucumis sativus*), sorghum (*Sorghum bicolor*), or tobacco (*Nicotiana tabacum*), contrasting with the results from Kohlen et al. (2011) who did report detection of SLs (orobanchol and orobanchyl acetate) from Arabidopsis and tomato xylem sap.

The effects of SL on shoot branching are mediated through a complex containing an α/β fold hydrolase SL receptor, AtD14/DAD2/RMS3/D14, and an F-box protein, MAX2/PhMAX2A/RMS4/D3, targeting SMXLs/PhD53A/D53 for ubiquitination and subsequent degradation, and downstream transcriptional targets include TFs such as BRANCHED1 (BRC1) and IDEAL PLANT ARCHITECTURE1 (IPA1; Ishikawa et al., 2005; Stirnberg et al., 2007; Hamiaux et al., 2012; Janssen and Snowden, 2012; Nakamura et al., 2013; Bennett et al., 2016; Figure 2). The SL receptor contains a canonical hydrolase catalytic triad in its cavity and has slow hydrolytic activity toward SLs, resulting in covalent attachment of a fragment of SL to the receptor protein (Hamiaux et al., 2012; de Saint Germain et al., 2016; Yao et al., 2016). This hydrolytic activity might occur after the perception of SL and signal transduction, as $AtD14^{D218A}$, a mutant for one of the catalytic triad residues, was able to complement the *atd14* mutant despite lacking hydrolytic activity (Seto et al., 2019).

D53 in rice and its homologs, SUPPRESSOR OF MORE AXILLARY GROWTH1-LIKE6,7, and 8 (SMXL6,7,8) in Arabidopsis are nuclear-localized SL-signaling repressors and are the primary targets of the SL receptor complex (Jiang et al., 2013; Zhou et al., 2013; Wang et al., 2015; Bennett et al., 2016). Phenotypes in single, double, and triple mutants of *SMXL6*, *SMXL7*, and *SMXL8* in Col-0 and the *max3* mutant background suggested that they function redundantly in promoting axillary bud outgrowth in Arabidopsis; however, there may be differences in the functions of the different SMXLs. For instance, SMXL6 can interact with MAX2 and AtD14 without GR24, while SMXL7 can interact with AtD14 only in the presence of GR24 (Wang et al., 2015; Liang et al., 2016). A recent study showed that SMXLs

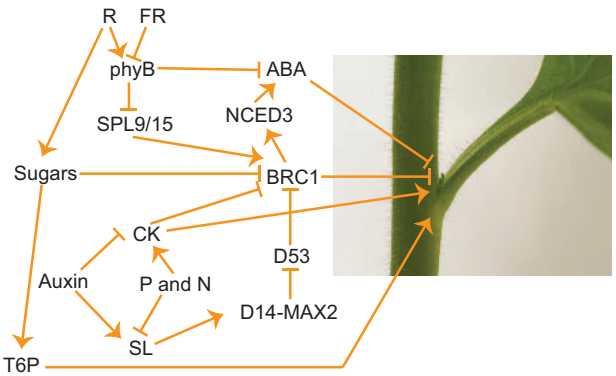

Figure 2 Selected components of axillary bud outgrowth regulation. Red light (R) promotes branching through phyB and SPL9/15 that regulate BRC1 (note FR is far-red light). Light quality also reduces ABA level, and increases sugar content, which suppresses BRC1 expression. Nutrient availability positively regulates CK content but negatively regulates SL production. SLs are transported at least partly by PDR1 and are perceived by the DAD2-MAX2-D53 complex. The degradation of D53 triggers BRC1 expression that inhibits axillary bud outgrowth. There are likely BRC1 independent pathways that involve T6P and SL and CK signaling. The arrows and blunt lines represent positive and negative regulation respectively.

function as TFs that repress their own transcription through direct binding to the promoters (Wang et al., 2020); meanwhile, SMXL6 is also able to interact with other corepressor/partner proteins, such as TOPLESS-RELATED PROTEIN (TRP) and SPL9 and SPL15 to repress the expression of *BRC1* (Wang et al., 2015, 2020; Xie et al., 2020). Similarly, it has been shown that D53 directly interacts with OsSPL14/IPA1 and TRP in rice and TaSPL17 in wheat (Liu et al., 2017; Ma et al., 2017; Song et al., 2017). D53 and SMXLs are able to regulate a number of targets (Wang et al., 2020); however, TFs such as BRC1/FC1/TB1 and SPLs also play a major role in the branching regulatory network.

As mentioned above, auxin and CK also play important roles in the branching regulatory network (reviewed in Muller and Leyser, 2011; Harrison, 2017; Barbier et al., 2019). In addition, it is clear that there is a role for abscisic acid (ABA) in regulating bud dormancy (Luo et al., 2019). Although BRs and GAs might not be considered to be part of the core hormone signaling pathway for controlling shoot branching (Bennett et al., 2016), recent evidence suggests they are part of the complex regulatory networks linking pathways and affect branching indirectly or as supplementary mechanisms (Ito et al., 2017; Fang et al., 2020; Zhang et al., 2020). In many plant species, further development of axillary buds into branches is suppressed by the influence of the primary shoot. The suppression mechanism of auxin on axillary bud outgrowth is yet to be fully elucidated, especially when auxin seems to act indirectly as it moves basipetally within the main stem and does not move into axillary buds (Muller and Leyser, 2011). Recently, a study indicated that at the initial stage, decapitation and CK induced bud outgrowth is independent of auxin flow from the bud (Chabikwa et al., 2019). Thus, auxin is likely to indirectly regulate branching by modulating other hormones such as CKs and SLs (Rameau et al., 2014; Barbier et al., 2019). Auxin positively regulates the expression of SL biosynthesis genes *CCD7* and *CCD8* in Arabidopsis, pea (*Pisum sativum*), and rice (Foo et al., 2005; Arite et al., 2007; Hayward et al., 2009) and, in turn, SL signaling modulates polar auxin transport and auxin biosynthesis (Hayward et al., 2009; Crawford et al., 2010; Shinohara et al., 2013; Ligerot et al., 2017).

There are several studies that suggest CK promotes branching in model species as well as woody perennials (Dun et al., 2012; Tan et al., 2019; and reviewed in Barbier et al., 2019). However, in some species, for instance *Rosa hybrida*, suppressing CK biosynthesis and signaling does not repress axillary bud outgrowth (Barbier et al., 2015). CK signaling results in a large number of transcriptional and other changes in relation to axillary bud outgrowth including changes in other hormone signaling pathways (Ni et al., 2017; Li et al., 2018; Waldie and Leyser, 2018). SL and CK regulatory pathways interact on a number of levels; first, at the transcriptional target level, both SLs and CK regulate the expression of *BRC1*, at least in Arabidopsis and pea (Dun et al., 2013); second, at the hormone production and degradation level, SLs have been shown to reduce CK levels through the transcriptional activation of *CYTOKININ OXIDASE/DEHYDROGENASE 9* in rice (Duan et al., 2019). In pea SL mutants (*rms1* and *rms4*), the expression of one of the CK biosynthesis genes, *ISOPENTYLTRANSFERASE1* (*IPT1*) was increased significantly compared with WT in node 3 of pea plants (Dun et al., 2012). These studies further support the cross talk among hormones during bud outgrowth.

The transcription factor BRC1 is a key regulator of branching in axillary buds

The most well-characterized transcriptional regulator in branching regulatory pathways is *BRC1* and its homologs in the TCP (TB1, CYCLOIDIA, and PROLIFERATING CELL FACTOR) TF family, including *tb1* of maize, *FINE CULM1* (*FC1*)/*OsTB1* of rice, *BRC1* and *BRC2* from Arabidopsis, and *PhTCP3* of petunia and *PsBRC1* of pea. These genes are expressed in axillary buds or in the leaf axils where axillary buds develop, where they can repress bud outgrowth without altering the number of axillary buds (Doebley et al., 1997; Takeda et al., 2003; Aguilar-Martínez et al., 2007; Finlayson, 2007; Minakuchi et al., 2010; Braun et al., 2012; Drummond et al., 2015; Nicolas and Cubas, 2016). Mutation and knock down of *BRC1* resulted in increased rosette branching in Arabidopsis (Aguilar-Martínez et al., 2007; Finlayson, 2007), strong basal branching in pea (Braun et al., 2012), and enhanced lateral tillering in rice (Takeda et al., 2003). *BRC1* expression is significantly higher in basal buds than apical buds and hence corresponded with branching (Finlayson, 2007; Drummond et al., 2015). The expression of *BRC1* is regulated by several pathways, such as SL and CK signaling, decapitation/auxin treatment, as well as sucrose treatment, nutrient availability, and light quality, and it is

thought to integrate many of these shoot-branching signals in flowering plants (reviewed in Teichmann and Muhr, 2015; Barbier et al., 2019; Wang et al., 2019).

It is important to note that *BRC1* is not the only mechanism that plants employ to inhibit branching (Figure 2). Not all nodes produce a branch in Arabidopsis *brc1 brc2* double mutants or pea *psbrc1* mutants, although they have twice as many or more branches than WT (Braun et al., 2012; Seale et al., 2017). The *brc1 bcr2* double mutant Arabidopsis plants are still sensitive to low N-induced and SL-induced branch suppression (Seale et al., 2017); however, this is in contrast to the *psbrc1* mutants in pea and *fc1* mutants in rice that are insensitive to SL treatment (Minakuchi et al., 2010; Braun et al., 2012). Moreover, CK can increase branch length in *psbrc1* mutants, suggesting CK has a *BRC1*-independent effect on sustaining bud outgrowth (Braun et al., 2012). The phenotypic difference between SL mutants and *brc1* mutants suggests that BRC1 is not the sole regulator for branching. The pea *rms1* mutant produced more branches at upper nodes, whereas *psbrc1* mutant plants had more branches at the basal nodes. In addition, the *rms1 psbrc1* double mutant had more branches than either *rms1* or *psbrc1* mutants at most of the nodes with the exception of node 2 (Braun et al., 2012). Similarly, in Arabidopsis, the *max4* or *d14* mutants had more branches than the *brc1 brc2* double mutant and the triple mutant had an additive phenotype (Chevalier et al., 2014; Seale et al., 2017). On the other hand, *fc1 d17* (an SL-deficient mutant) double mutant rice had a similar phenotype to *d17* single mutants and GR24 application had no significant effect on the expression of *FC1* (Minakuchi et al., 2010). A recent study suggested that ABCB19, an auxin transporter, might respond to GR24 but acts on a separate pathway from BRC1 (van Rongen et al., 2019). These observations suggest that BRC1/FC1/TB1 acts downstream of, but not exclusive to, the SL-signaling pathway, and that BRC1-independent branching regulation is likely, but yet to be identified and characterized.

Despite recent progress, our knowledge of the mechanism of action for *BRC1* inhibition of bud growth remains incomplete. There are a number of possible routes downstream of *BRC1* leading to bud growth inhibition. Recently, Shen et al. (2019) found that CsBRC1 in cucumber directly binds to the *CsPIN3* promoter to repress the transcription of *PIN-FORMED3* (*PIN3*), an auxin efflux carrier, possibly leading to reduced auxin export from axillary buds and subsequently suppression of branch outgrowth. BRC1 proteins are also able to bind to three HD-ZIP encoding genes, *HB21*, *HB40*, and *HB53* to up-regulate their expression, resulting in up-regulation of *9-CIS-EPOXICAROTENOID DIOXIGENASE 3* (*NCED3*) and accumulation of ABA, causing inhibition of branch outgrowth (González-Grandío et al., 2017). *BRC1* expression was not affected by ABA application, further supporting the idea that ABA signaling in branching regulation is downstream of BRC1 (Yao and Finlayson, 2015). More recently, Luo et al. (2019) provide further evidence of the role of ABA in the downstream regulation of bud dormancy, and this action is expected to be BRC1 dependent in some species (Wang et al., 2020).

Axillary branching is highly plastic in response to environmental signals

Our understanding of how the environment, especially nutrient concentrations and light quality, influence branching has advanced rapidly thanks to powerful genetic screening and transcriptomic tools (Figure 2).

Phosphate (P) and nitrogen (N) are the two macronutrients that limit plant growth and yield potential, and limited supply of N and/or P modulate root architecture, shoot branching, and flowering time through regulation of hormones and transcriptional changes (Péret et al., 2014; Ham et al., 2018; Luo et al., 2020). Hormones, especially SLs, are affected by nutrient availability (Umehara et al., 2008; Mayzlish-Gati et al., 2012; Al-Babili and Bouwmeester, 2015; Luo et al., 2020). Limited availability of P, N, and sometimes sulfur promotes SL production in, and exudation from, the roots, upregulates expression of SL biosynthetic genes, and inhibits branching in a number of species (Yoneyama et al., 2007, 2012; Drummond et al., 2015; Abuauf et al., 2018; Shindo et al., 2018). Conversely, P and N fertilization suppresses the expression of SL biosynthesis genes and subsequent SL exudation and increases branching (Umehara et al., 2008; Yoneyama et al., 2013, 2020). However, SL content is not the sole regulator of branching in response to low-nutrient conditions, as branch numbers were still reduced in SL-deficient and insensitive mutants of petunia under low-P or low-N conditions (Drummond et al., 2015). Indeed, there are reports indicating that low levels of P and N reduce CK production and signaling (reviewed in Wang et al., 2019). Low-N levels also reduced the branch angle in petunia (Drummond et al., 2015); however, the underlying mechanism is largely unknown.

Light quality is another environmental input that can greatly alter plant branching. When the red-to-far-red light (R:FR) ratio decreases, phytochrome (phy) proteins sense the change and trigger the shade-avoidance syndrome (Franklin, 2008; Franklin and Quail, 2010), suppressing axillary bud outgrowth in several plant species, similar to the *phyB* mutant phenotype in Arabidopsis and sorghum (Kebrom et al., 2006; Finlayson et al., 2010; Whipple et al., 2011; Reddy et al., 2013; Drummond et al., 2015). At least part of the branching response to changes in light is mediated by the SL pathway. MAX2, an F-box protein that is part of the SL receptor complex, is involved in photomorphogenesis regulatory pathways in Arabidopsis, and, in petunia, SL pathway mutants have increased branching in altered light conditions (day length, and R-FR changes as well as crowding (Snowden and Napoli, 2003; Shen et al., 2007; Drummond et al., 2015)). In addition to regulating branch outgrowth, light appears to have a role in regulating branch angle in petunia (Snowden and Napoli, 2003;

Drummond et al., 2015), in Arabidopsis through promoting the expression of *TILLER ANGLE CONTROL* (*TAC1*; Waite and Dardick, 2018), and in maize through supressing the expression of *ZmLAZY1* (*ZmLA1*, Dong et al., 2013).

The mode of action for nutrient and light regulation of branching in axillary buds is largely mediated through *BRC1* and its homologs. FR light increased the expression of *DAD2* and *PhTCP3* expression in petunia axillary buds (Drummond et al., 2015) as well as the expression of *BRC1* and *BRC2* in Arabidopsis and sorghum axillary buds (Kebrom et al., 2006; Finlayson et al., 2010; Gonzalez-Grandio et al., 2013; Xie et al., 2020). *CsBRC1* transcript was enhanced after shade treatment in the inbred less-branched cucumber line R1461, whereas shading had little effect on the highly branched wild ancestor cucumber variety (Shen et al., 2019). In perennial crops, day length and temperature also contribute to shoot branching. Short days and low temperatures suppressed branching in *Populus* by up-regulating the expression of *BRC1* and *TERMINAL FLOWER 1/CENTRORADIALIS 1* (*TFL1/CEN1*, Maurya et al., 2020). There is also some evidence to support the control of *BRC1* by nutrients like P and N; for instance, supply of nitrate enhanced the expression of *OsMADS57*, a MADS-box TF, which interacts with OsTB1 and targets D14 (a SL receptor) to regulate tiller outgrowth in rice (Guo et al., 2013; Huang et al., 2019). The nutrient regulation of *BRC1* might also be mediated through hormone biosynthesis and signaling, including SLs, CK, and auxin.

Sugars have been shown to promote axillary bud outgrowth as observed in rice, pea, Arabidopsis, and chrysanthemum, with increasing evidence for the role of trehalose 6-phosphate (T6P) in this process (Mason et al., 2014; Fichtner et al., 2017, 2020; Barbier et al., 2019; Liu et al., 2020; Wang et al., 2020). Sugar availability is tightly linked to the carbon-fixation process that is heavily dependent on light quality. For example, removing leaves suppressed bud outgrowth in sorghum and pea, and girdling above the bud had the same effect on preventing branching in pea (Mason et al., 2014; Kebrom and Mullet, 2015). Sugars can act through *CIRCADIAN CLOCK ASSOCIATED1* (*OsCCA1*) to regulate branching via the SL pathway and *OsTB1* in rice (Wang et al., 2020). However, at least in Arabidopsis, branching changes due to alterations of T6P are additive with the *brc1* mutation, indicating that sugars probably affect multiple pathways that control branching (Fichtner et al., 2020).

Concluding remarks

The growth of an axillary meristem to form a branch is a costly exercise that must balance the resources available with the current environmental conditions. A dynamic environment, especially one with changing nutrients and light quality, can lead to a range of shoot branching outcomes, from a high degree of active axillary meristem outgrowth to strong suppression of branching. In this context, different axillary meristems in a single plant can have dramatically different growth outcomes, ultimately affecting the overall shape of a plant. Over the last three decades, our knowledge of individual processes controlling axillary meristem initiation and branch growth has become increasingly detailed. However, the goal of integrating all our observations into the complex network of regulation is still incomplete (see Outstanding questions). Using model species to answer these questions has been extremely informative, but one particular challenge remains, given increasing stresses on the world's food supply, how to control precisely the growth of specific branches in cultivated crops and perennial species, with the goal of enabling greater sustainable food production.

OUTSTANDING QUESTIONS

- How much regulation of axillary meristem initiation is conserved between monocots and eudicots?
- What determines the different growth outcome of axillary buds that are located at different positions on the main shoot?
- Is there a developmental trigger that makes a meristem competent for outgrowth?
- How are all the different signals involved in meristem growth integrated?
- How do axillary meristem cells initiate the outgrowth process?
- How do we get the diversity of form observed in plants, given the evolutionary conservation of the signal transduction pathways discussed here?
- How can developmental plasticity be used to improve crop yield?

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