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Review

Conservation and divergence: Regulatory networks underlying reproductive branching in rice and maize

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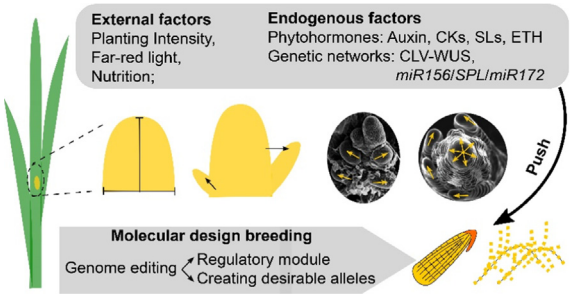
HIGHLIGHTS

- Branching pattern in maize and rice determines the inflorescence architecture and thus the final grain yield.
- The branching pattern is determined by meristem size, bud initiation and outgrowth, and controlled by endogenous and external factors.
- Genetic control of inflorescence branching including CLV-WUS feedback loop, Auxin-cytokinin crosstalk and *miR156*/*SPL*/*miR172* in maize and rice is summarized.
- The comprehensive genetic networks associated with crop branching, will promote the transformation of molecular designs breeding based on regulatory networks via genome editing, then produce optimized inflorescence architecture.

GRAPHICAL ABSTRACT



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ABSTRACT

Background: Cereal crops are a major source of raw food and nutrition for humans worldwide. Inflorescence of cereal crops is their reproductive organ, which also contributes to crop productivity. The branching pattern in flowering plant species not only determines inflorescence architecture but also determines the grain yield. There are good reviews describing the grass inflorescence architecture contributing to the final grain yield. However, very few discuss the aspects of inflorescence branching.

Aim of review: This review aimed at systematically and comprehensively summarizing the latest progress in the field of conservation and divergence of genetic regulatory network that controls inflorescence branching in maize and rice, provide strategies to efficiently utilize the achievements in reproductive branching for crop yield improvement, and suggest a potential regulatory network underlying the inflorescence branching and vegetative branching system.

Key scientific concepts of review: Inflorescence branching is the consequence of a series of developmental events including the initiation, outgrowth, determinacy, and identity of reproductive axillary meristems, and it is controlled by a complex functional hierarchy of genetic networks. Initially, we compared the inflorescence architecture of maize and rice; then, we reviewed the genetic regulatory pathways

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controlling the inflorescence meristem size, bud initiation, and outgrowth, and the key transition steps that shape the inflorescence branching in maize and rice; additionally, we summarized strategies to effectively apply the recent advances in inflorescence branching for crop yield improvement. Finally, we discussed how the newly discovered hormones coordinate the regulation of inflorescence branching and yield traits. Furthermore, we discussed the possible reason behind distinct regulatory pathways for vegetative and inflorescence branching.

Introduction

Cereal crops are one of the most cultivated plant species in the world. Maize (*Zea mays* L.) and rice (*Orzya sativa* L.), two vital grass species, are sources of carbohydrates and play important roles in human food, animal feed, bioenergy, and industrial raw materials. Rice is domesticated in subtropical regions and widely grown in lowlands [1]. While maize is domesticated in tropical regions and widely grown in uplands [1]. In addition, a single rice plant contains multiple tillers, each of which has one panicle initiated from a shoot apical meristem [2]. In maize, however, a single plant has one main stem with one tassel and one to two ears. Tassel usually initiates from shoot apical meristem and ears are generated from leaf axillary meristem [3]. Inflorescence in flowering plant species is the reproductive organ that differentiates from apical meristem after the vegetative-to-reproductive transition [4]. Grass inflorescence comprises of different branches that are developed from branch meristems (BMs), a type of axillary meristems (AMs); then, a set of spikelets or florets is generated on each branch in a stereotyped pattern [4]. This suggests that the number of spikelets and florets directly affects the number of branches and ultimately the grain number.

In the last few decades, scientists have characterized several genes that control reproductive branching. This improved our understanding of the genetic basis and molecular regulatory networks of reproductive branching in cereal crops. Maize and rice have different plant architecture. However, the developmental process of reproductive branching seems to be conserved to some extent. There are excellent reviews that have summarized the genetic basis for the regulation of shoot branching [5,6], grass inflorescence architecture [3,4,7,8], etc. However, very few of them have focused on the reproductive branching and grain yield of crops. In this review, we summarized the conservation and divergence in the regulatory networks of reproductive branching in rice and maize. Furthermore, we have suggested strategies to effectively exploit the latest developments in crop breeding.

The similarities and differences of maize and rice inflorescence development

Inflorescence in grass species has a typical compound spike consisting of different types of branches and spikelets,where each spikelet can produce one to multiple florets [9,10]. Inflorescence meristem (IM) originates from the central rachis and then initiates indeterminate BMs, which in turn produce a series of spikelet meristems (SMs). This process terminates with the development of determinate or indeterminate floral meristems (FMs), depending on the species [4,10] (Fig. 1AE). This differentiation pattern is identical in maize tassel inflorescence and rice panicle, resulting in similar branching architecture including primary branches (PBs) and secondary branches (SBs) (Fig. 1BF).

A question arises regarding the cause of the architectural difference between them. First, the shape of maize ear inflorescence and rice panicle is very different; the ear IM that formed from the vegetative AM initiates determinate spikelet pair meristems (SPMs) directly (Fig. 1C), instead of indeterminate BMs that form long branches [11,12]. Therefore, corn kernels are formed and attached to the ear cob, instead of the terminal of main rachis or on the branches like rice grains (Fig. 1D). Furthermore, in maize, the determinate SPMs are formed on the BMs and each SPM will initiate two SMs that make the double-ranked kernels on the ear cob (Fig. 1AC). In rice however, SMs attach on the BMs directly [11-13] (Fig. 1E). Finally, a maize SM produces two unisexual flowers (upper and lower flowers), whereas each rice SM generates only one bisexual flower with stamen and pistil [4,13] (Fig. 1G). Thus, the branching system of maize ear inflorescence and rice panicle are distinct. This provides an opportunity to elucidate the conserved and diverged mechanisms involved in the regulation of branching in both species.

Conservative CLAVATA-WUSCHEL feedback loop regulates maize and rice inflorescence branching

Plant organs originate from the meristem, a group of totipotent and indeterminate stem cells. The proliferation and differentiation of stem cells determine the size of the meristem, which gives the space to produce AMs. The process is regulated by a complex network, such as the canonical CLAVATA (CLV)-WUSCHEL (WUS) feedback loop. In *Arabidopsis*, the homeodomain transcription factor WUS, required for the stem cell formation and maintenance, is expressed in a small group of cells in the organizing center (OC) below the stem-cell domain [14,15]; while a small and mobile CLV3/ESR-related (CLE) peptide, which initiates new organ primordia on the flanks [16,17], is expressed in the peripheral zone. *WUS* promotes *CLV3*/*CLE* expression and *CLV3*/*CLE* represses WUS activity *via* CLV1 receptor-like kinase or CLV2 receptor-like proteins. This forms a negative feedback loop and thus, maintains an organized meristem niche [17-21].

In recent decades, several homologous proteins controlling the inflorescence meristem size and branches have been identified in maize and rice that provides evidence for the conservation of the receptor-ligand complexes in the CLV-WUS pathway in both species. There are *Arabidopsis* CLV homologous proteins, such as CLV1 homolog THICK TASSEL DWARF1 (TD1) in maize [22] and FLORAL ORGAN NUMBER1 (FON1) in rice [23]; CLV2 homolog FASCIATED EAR2 (FEA2) [24], CLV-type leucine-rich repeat (LRR) receptor-like protein FEA3, and additional four potential CLV3-like factors FON2-LIKE CLE PROTEIN1 (ZmFCP1) [25], the CLAVATA3-EMBRYO-SURROUNDING REGION (CLE) peptides ZmCLE7, ZmCLE14, and ZmCLE1E5 [26] in maize (Fig. 2A), and four CLV3-like factors FON4/2, FON2 SPARE1 (FOS1), FCP1, and FCP2 [27-30] in rice (Fig. 2B). Mutation of any *CLV* genes results in similar phenotypes with an enlarged IM, a thickened rachis, and an increased number of floral organs in both species. This indicates the functional conservation of those CLV receptors in both species. The diversity of interaction between CLV receptors and CLE peptides, and species-dependent downstream pathways regulated by CLV-WUS have been clearly identified. In *Arabidopsis*, the CLV3 peptides are independently perceived by two parallel pathways: CLV1 or CLV1-related LRR receptor-like kinase (LRR-RLKs) homod-

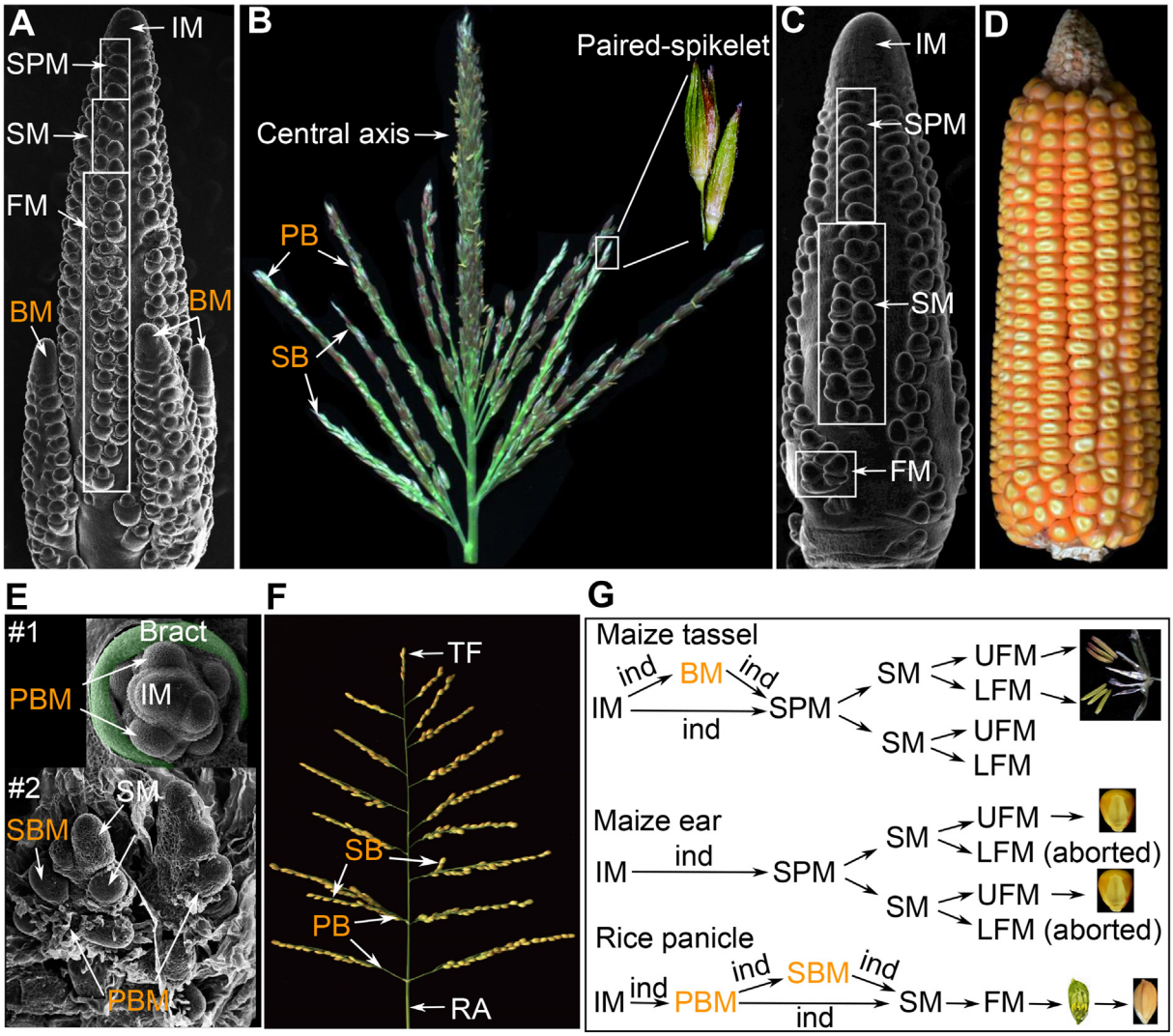

Fig. 1. Maize and rice inflorescences. (A, C, E) The scanning electron microscope images of maize male (A), female (C) inflorescences and rice panicle (E), showing reproductive axillary meristems. (B, D, F) Architecture of mature inflorescence of maize tassel (B) and ear (D), and rice panicle (F), showing primary and secondary branches. (G) Developmental processes of inflorescences in maize and rice. The branches (meristem) are indicated in orange. IM, inflorescence meristem; BM, branch meristem; SPM, spikelet pair meristem; SM, spikelet meristem; UFM/LFM, up/low floral meristem; PB(M), primary branch (meristem); SB(M), secondary branch (meristem); TF, terminated floret; RA, rachis; ind, indeterminate.

imers and CLV2-CRN (CORYNE) heterodimer [21]. Similarly in maize, the specific receptor-ligand pairings are ZmFCP1-FEA3 and ZmCLE14-TD1 [31]. In addition, ZmCLE7 and ZmFCP1 peptides are proposed to bind FEA2-COMPACTPLANT2 (CT2) - G protein β subunit (ZmGβ) and FEA2-ZmCRN receptor complexes, respectively [24,31,32] (Fig. 2A). In rice, FON4/2 peptides are perceived by FON1 and additional receptor-like proteins [27,28]. However, the receptors of FCP1, FCP2, and FOS1 peptides and their downstream components are still unknown in rice.

Interestingly, *WUS* is required for stem cell formation and maintenance in *Arabidopsis*, However, the functional counterparts of *WUS* have still not been clearly identified in maize and rice. *ZmWUS1* and *ZmWUS2* are *Arabidopsis WUS* homologs in maize, and *OsWUS*/*TAB1* (*TILLERS ABSENT1*)/*MOC3* (*MONOCULM 3*)/*SRT1* (*STERILE AND REDUCED TILLERING 1*)/*DC1*(*decreased culm number 1*) are *Arabidopsis WUS* homologs in rice [33-37]. *ZmWUS1* is expressed in OC-like region of the IM (Fig. 2A), while the expression domain of *ZmWUS2* is unclear [25]. Ectopic overexpression of *ZmWUS1* leads to stem cell over-proliferation. However, the reproductive AM initiation is strongly repressed, resulting in the formation of ball-shaped ears [38], indicating that *ZmWUS1* is involved in both meristem maintenance and AM initiation. *ZmWUS2* and other *WOXs* (*WUSCHEL-RELATED HOMEOBOXs*) might work redundantly with *ZmWUS1* because the knockout of *ZmWUS2* did not result in any phenotypic changes [38]. Interestingly, the past transcripts analyses and single-cell RNA sequencing could not detect the expression of *ZmWUS* genes in the shoot apical meristem (SAM) [39-41], inferring that canonical CLV-WUS pathway is bypassed in the SAM. Rice *TAB1*/*MOC3*, a WUS-encoding gene that is expressed in the pre-meristem zone in rice is negatively regulated by *FON2* and determines AM initiation. However, it is not involved in the SM or FM maintenance [13,34] (Fig. 2B). Interestingly, *OsWOX4* (*WUSCHEL-RELATED HOMEOBOX4*) is widely expressed in the meristem during the vegetative-to-reproductive stage transition. Loss-of-function *oswox4* mutant showed a premature termination of the meristem [42]. These results suggest that *WUS* is required for AM maintenance in rice and maize.

Genes in the CLV-WUS pathway have a specific expression domain. Maize *TD1* is expressed in the lateral primordia and all the reproductive meristems. Thus, the *td1* mutant displays a

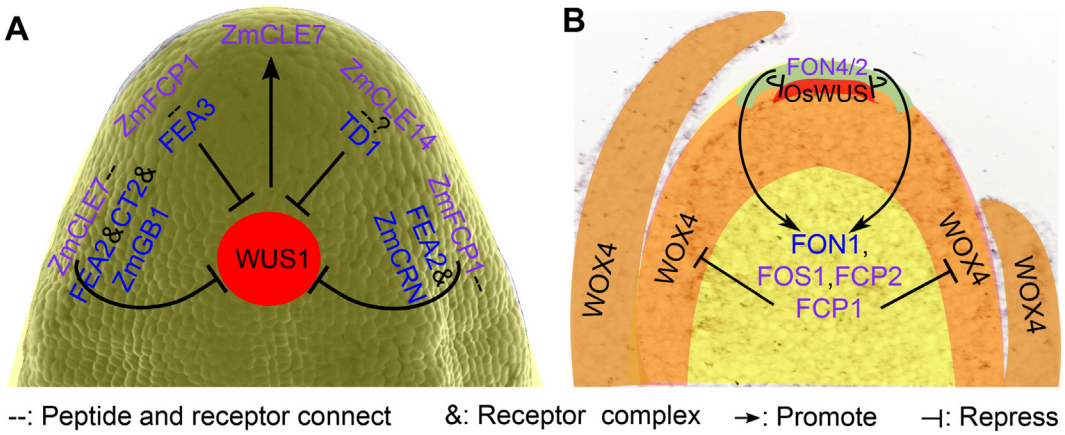

Fig. 2. CLAVATA-WUSCHEL negative feedback loop controls the inflorescence meristem size in maize (A) and rice (B). Maize *WUS1* is weakly expressed in the center of the inflorescence meristem to promote the expression of *CLAVATA3-EMBRYO-SURROUNDING REGION7* (*CLE7*). Four peptides and receptor complex containing ZmFCP1-FEA3, ZmCLE14-TD1, ZmCLE7-(FEA2-CT2-ZmGB1), and ZmFCP1-(FEA2-ZmCRN) restrict *WUS1* in a small domain. *OsWUS* is expressed in the pre-meristem zone, which includes several cell layers under the expression domain of *FLORAL ORGAN NUMBER4/2* (*FON4/2*) at the tip of axillary meristems. The expression of *OsWUS* is repressed by *FON4/2*. Rice *WUSCHEL-RELATED HOMEOBOX4* (*WOX4*) is strongly expressed in the peripheral zone of the inflorescence meristem and leaf primordia. The peptides are indicated in purple and receptors in blue. Genes mentioned above are also listed in Supplementary Table 1.

widely defective phenotype with a thickened inflorescence and increased floral organs [22]. Rice *FON1*, an ortholog of maize *TD1*, is expressed throughout the vegetative and reproductive meristems including the embryo, SAM, IM, and FM. However, the *fon1* mutant only displays an enlarged floral meristem and ectopic floral organs. Defective phenotype is not observed in SAM and IM [23], suggesting the possible function compensation by an additional uncharacterized CLV1-like proteins in the SAM and IM of rice. Identifying and characterizing more receptor-ligand pairs will provide deeper insights into the CLV-WUS pathway in rice and present subtle similarities with maize and other cereals. Although the functions of the *CLV* genes are conserved in modulating the size of IM in maize and rice, the biological roles of *WUS* genes and their upstream genes need to be further explored. Notably, the formation of enlarged IM and shorter branches by disrupting the components of the CLV-WUS feedback loop could be exploited. Thus, desirable alleles of genes in the CLV-WUS feedback loop could be artificially created by genome editing to enhance the inflorescence size, thereby improving the crop yield.

Phytohormones mediate maize and rice inflorescence branching pattern

The reproductive branches in grasses originate from the AMs in the axils through a two-step process: initiation of BMs and their subsequent outgrowth (Fig. 1E, Fig. 2A). In maize, long and short branches are formed from the BMs in tassel and SPMs in ear, respectively. The branching pattern in rice panicle is created by the formation of primary BMs (PBMs) from the IM, and secondary BMs (SBMs) from the PBMs [3] (Fig. 1E and 1G). Phytohormones are comprehensively involved in the regulation of branching patterns in both species.

Auxin mediates AM initiation and outgrowth in maize and rice

Auxin is required for the initiation and outgrowth of new organs from meristems in plants. Genes involved in auxin biosynthesis, transport, and their roles in the reproductive branching system are conserved across angiosperms. *Arabidopsis YUCCA* (*YUC*) and *Tryptophan Aminotransferase 1* (*TAA1*) are two key genes in the tryptophan-dependent auxin biosynthesis. Their orthologs are *SPARSE INFLORESCENCE1* (*SPI1*) and *VANISHING TASSEL2* (*VT2*) in maize [43,44], *OsYUCCA1* and *OsYUC1-14* and *Tryptophan Deficient Dwarf1* (*TDD1*) in rice [45,46] (Fig. 2B; Table 1; Supplemental table 1). Any loss-of-function mutants of these genes exhibits a low auxin level. Thereby, demonstrating the functional conservation in auxin biosynthesis. However, they have different effects on inflorescence or plant architecture based on their specific expression patterns or organogenesis divergence in maize and rice. For example, *VT2* is specifically expressed in the epidermis of the IM and SPMs (Fig. 3C); *vt2* mutant exhibits sparse or barren inflorescences with fewer branches or spikelets [44]. Rice *TDD1* is expressed in the tips of leaves, roots, and vascular bundles; its mutant *tdd1* produces abnormal flowers and dwarf plants with narrow leaves [45].

Auxin distribution is not homogeneous in the meristem cells. Auxins are transported towards the meristem peripheral zone to establish local maxima for lateral organ formation, which is mediated by a series of auxin influx and efflux carriers. Rice PINOID (OsPID), a serine/threonine protein kinase, regulates auxin distribution through the positive control of subcellularly localized PINs. Unlike the *pid* mutant that shows typical pin-like inflorescences in maize, the *ospid* mutant does not show any defects in the inflorescence or flower [47]. The PIN1 family genes include *ZmPIN1a* and *ZmPIN1b* in maize [48] and *OsPIN1*, *OsPIN1b,* and *OsPIN1c* in rice [49] (Table 1). Maize BARREN INFLORESCENCE2 (BIF2) encodes a PINOID serine/threonine kinase that phosphorylates ZmPIN1a to redistribute the auxins [50]. The expression domains of *ZmPIN1a* and *BIF2* are mostly consistent in all the AMs and lateral primordia during the vegetative and reproductive development The *bif2* mutant exhibits repressed initiation of both the AMs and lateral primordia [50,51] (Fig. 3AB). In rice, besides *OsPID* and *OsPIN* genes, *PLANT ARCHITECTURE AND YIELD 1* (*PAY1*) [52], *Lazy1* [53], and *Big Grain1* (*BG1*) [54] are well implicated in polar auxin transport and AM development. However, the orthologs for *PAY1* and *BG1* are not yet characterized in maize. Assessing their expression patterns and functions in the inflorescence development *via* an auxin-mediated pathway can be a future endeavor in maize.

The auxin signaling pathway involves several genes (Table 1). Downstream of the auxin regulation, ortholog gene pairs, including *BARREN STALK1* (*BA1*) and *BA2* In maize [55,56], and *LAX PANICLE1* (*LAX1*) and *LAX2* in rice [57,58], function in different pathways in the AM formation (Fig. 3B; Table 1; Supplemental table 1). Both *BA1* and *LAX1*, showing boundary expression patterns, are core factors in the regulation of AMs. In the *BA1*-auxin response network, the expression switch of *BA1* is dependent on the RAMOSA1 ENHANCER LOCUS2 (REL2)-BARREN INFLORESCENCE1/4 (BIF1/4)-

Table 1
Genes associated with the auxin metabolism and signaling pathway in *Arabidopsis*, maize, and rice.

Auxin pathway	*Arabidopsis*	Maize	Rice
Auxin Biosynthesis	*TAA1*	*VT2*	*TDD1*
	YUC	*SPI1*	*OsYUCCA1*
			OsMED14_1
Auxin Transport	*PID*	*BIF2*	*OsPID*
	PIN	*ZmPIN1a, ZmPIN1b*	*OsPIN1a/1b/1c/1d, OsPIN2, OsPIN5a/5b/5c, OsPIN8, OsPIN9, OsPIN10a/10b*
			PAY1, Lazy1, BG1
Auxin Signal	–	*BIF1, BIF4,* ***BAF1, FEA4***	*Aux/IAA*
	–	*BA1,* ***BA2***	*LAX1, LAX2*
	–	***REL2***	*ASP1*
	AtARFs	*ZmARFs*	*OsARFs*
			OsAFBs

Note: Genes in bold font are involved in the auxin pathway indirectly.

ZmAUXIN RESPONSE FACTORs (ZmARFs) complex [59] (Fig. 3B; Table 1; Supplemental table 1), where *ZmARFs* are positively regulated by the MALE STERILE CONVERTED ANTHER1 (MSCA1)-FEA4 complex [60]. BIF2 physically interacts with BA1 that is positively regulated by *BARREN STALK FASTIGIATE1 (BAF1)* [61]. Any mutant of these identified genes exhibit auxin deficiency phenotype with decreased number of branches and spikelets. In rice, single mutants of *LAX1*, *LAX2*, and *MOC1* have reduced inflorescence branches and spikelets, and the double mutants of *lax1moc1*, *lax2-moc1*, and *lax1lax2* enhance the reduced-branching phenotype, which indicates that *LAX1*, *LAX2*, and *MOC1* regulate panicle architecture in multiple pathways [57,58,62]. LAX2 physically interacts with OsIAA3 and interferes with the interaction of OsIAA3-OsARF2, which may de-repress *OsARF25* and enhance the transcription of its downstream target genes [63]. Whereas LAX1 physically interacts with OsPID which may regulate polar auxin transport [64]. In contrast to *BA1* network in maize, *LAX1-LAX2-MOC1* regulates the tillers number during the vegetative stage. This difference could be caused by the gene specific expression pattern in different species.

Most genes identified in maize inflorescences are broadly expressed in the peripheral zone of the meristems. However, some of them are specifically present in the cells of the outer layer. Unlike *BIF2* and *BA2* expressed throughout the meristem, *BIF1* is expressed only in the abaxial domain. Whereas, *SPI1*, *BA1*, and *BAF1* are expressed in the adaxial domain of AMs and *BIF4* is expressed in the center domain of the ear inflorescence meristem, showing a complementary expression pattern [55,56,65,66] (Fig. 3C). Both the boundary domain expression genes and the center domain expression genes have the same function in directing maize branch formation, indicating that there could be mobile signals from the abaxial, adaxial, and central domain of the tissue,

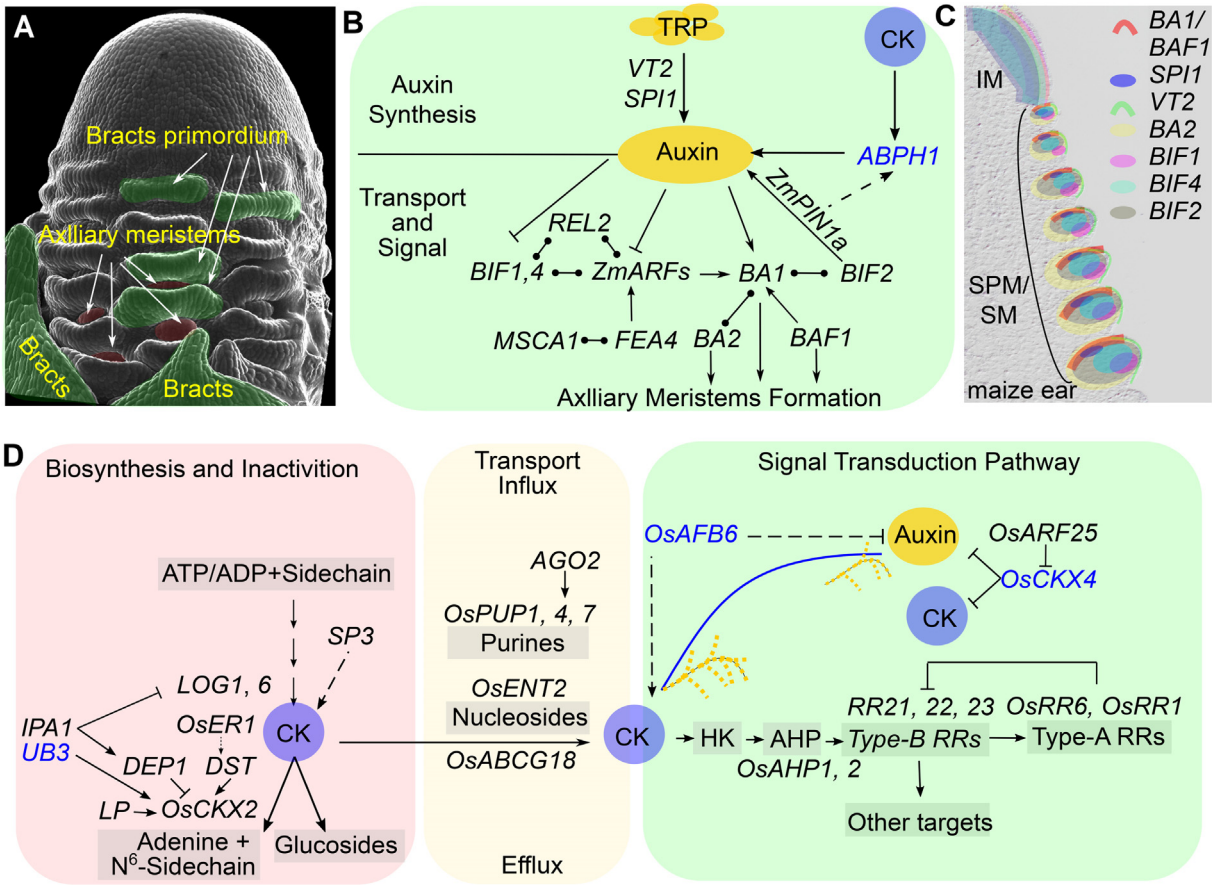

Fig. 3. Auxin and cytokinins regulate the meristem size and axillary bud outgrowth. (A) Scanning electron microscope image of 1–2 mm maize inflorescence meristem with suppressed bract primordia and developing axillary meristem. (B) Genes associated with the auxin biosynthesis, transport, and signal pathway, regulating the inflorescence branching in maize. Genes indicated in blue color are involved in the coordination between auxin-cytokinins signal. (C) The expression domain of key genes in (B). (D) Genes associated with the cytokinins biosynthesis, transport, and signal pathway, regulating the inflorescence branching in rice. Genes indicated in blue color represent maize genes or those coordinating the auxin-cytokinins signal. In the green frame, a higher ratio of cytokinins/auxin leads to large panicles with more branches in rice. Genes mentioned above are also listed in Supplementary Table 1.

forming a complex network to regulate meristem activity [8], or they have complementary functions in the AMs initiation. In rice, the movement of LAX1 protein regulating new AMs initiation is a good example of such mobile signals [57]. Other rice inflorescence expressed genes such as *LAX2*, *TAB1/MOC3*, and *MOC1* are expressed in the boundary domain of the IM, along with those in the vegetative AMs and control the outgrowth of tiller buds. Probably, the expression of these genes in specific domains triggers organogenesis from the corresponding meristems [34,58,62]. This could be the reason why rice has vegetative branching (tillering), but maize has unique stem without vegetative branching, which results in a very different plant architecture.

Cytokinin modulates the inflorescence/panicle branching

Cytokinins (CKs), which are synthesized in the roots and transported to the shoots, modulate the inflorescence branching by promoting cell proliferation. The biosynthesis and degradation of CKs are regulated by multiple inputs, including members of the *LONELY GUY* (*LOG*) that catalyze the conversion of inactive cytokinin nucleotides to the active free-base forms and cytokinin oxidase/dehydrogenase (CKX) family for CKs deactivation [67] (Fig. 3D; Supplemental table 1). The single mutant of rice log or *cytokinin oxidase2* (*Osckx2/gn1a*) exhibits a variable number of branches and spikelets, depending on the CKs level in the panicle [68,69]. Several genes, such as *DENSE AND ERECT PANICLE1* (*DEP1*) [70], *DROUGHT AND SALT TOLERANCE* (DST) [71], and *LARGER PANICLE* (*LP*) [72] are involved in the regulation of *OsCKX2* expression (Fig. 3D; Supplemental table 1). *DEP1* encodes a G-gamma subunit; the truncated DEP1 promotes branching and increases the grain number by repressing the *OsCKX2* expression [70]; while both DST and *LP* reduce active CKs levels by upregulating *OsCKX2* and results in a decrease of branches and grains per panicle [71,72]. An *OsCKX2*-centered network for the regulation of the reproductive branching is clearly exhibited in rice (Fig. 3D; Supplemental table 1). Meanwhile, *DEP1* is positively regulated by rice *IDEAL PLANT ARCHITECTURE1* (*IPA1*), a gene that encodes SQUAMOSA promoter binding protein (SBP)-like transcription factor [73,74]. Interestingly, maize *UNBRANCHD3* (*UB3*), the ortholog of *IPA1*, is one of the direct targets of GRF-interacting factor1 (GIF1) [75] and negatively regulates the initiation of lateral primordia in inflorescences by functioning together with two additional SBP-box family genes: *UNBRANCHD2* (*UB2*) and *TASSELSHEATH4 (TSH4)* [76,77]. When *UB3* cDNA is introduced in rice, it modulates the panicle branches by regulating the expression of *LOG* and *OsCKX2* [78]. Therefore, the function of *UB3/IPA1* mediated CKs signals in inflorescences is conserved in both maize and rice (Fig. 3D).

In general, root-derived CKs are transported to shoots *via* efflux and influx carriers: equilibrative nucleotide transporter (ENT), purine permease (PUP), and three ATP-binding cassette G (ABCG) transporter families. *OsENT2* [79], *OsPUP1*, *4*, *7*, [80-82] and *OsABCG18* [83] are considered as the long-distance transporters of the root-derived CKs, transporting them towards the shoot and modulate tiller numbers, panicle branches, and grain yield by transporting tZ-type CKs (Fig. 3D; Supplemental table 1). ARGONAUTE2 (AGO2), which is an established factor of the microRNA-induced silencing complex, increases the grain length by activating *OsPUP4*, which modulates CKs distribution in rice [84] (Fig. 3D; Supplemental table 1). However, in contrast to the well-established transport mechanisms of auxin, the mechanisms of directional transporting of CKs are not well known. *De novo* CKs biosynthesis takes place only in specific cell types; therefore, CKs have to be delivered to the target cells for signaling [85]. Thus, elucidating the molecular mechanism of CKs loading is essential for understanding the pathways of CKs signaling. The type-B response regulators (type-B RRs) and type-A RRs are critical components of the CKs signaling. The type-B RRs promote transcriptional response to CKs by activating *WUS* expression [86,87]. Whereas, type-A RRs act as negative-feedback regulators of CKs [88]. Rice mutants *rr21*, *rr22*, and *rr23*, which have decreased activity of the type-B RRs, show reduced primary and secondary branches and panicle length [87]. In contrast, overexpression of the rice type-A *OsRR6* represses CKs signaling, leading to smaller inflorescences [88] (Fig. 3D).

Crosstalk between auxin and CKs determines the inflorescence branching

The long-term stem cell self-renewal and differentiation is coordinately regulated by CLV-WUS signal, local auxin/CKs levels and their distribution, suggesting an auxin-WUS-CKs crosstalk. In *Arabidopsis*, *WUS* acts as a rheostat to modulate the local auxin levels in the CZ through regulating *ARFs* and histone acetylation, and represses CKs by targeting the type-A *ARRs* (*ARR5*, *6*, *7*, *15*) [89-91]; while auxins activate *WUS* transcription through *ARF5*/*MONOPTEROS* (*MP*) *-DORNROSCHEN/ENHANCER OF SHOOT REGENERATION 1* (*DRN*/*ESR1*)*-CLV3* pathway and CKs promote *WUS* expression through the Type-B *ARRs* (*ARR1*, *10*, *12*) [85,92,93] (Fig. 4). *WUS* also promotes the expression of *SHOOT MERISTEMLESS* (*STM*), which in turn up-regulates the levels of CKs by activating the expression of *ISOPENTENYLTRANSFERASE 7* (*IPT7*) [94] and thus, make a border CK signaling-rich (CSR) region. ARABIDOPSIS HISTIDINE PHOSPHOTRANSFER PROTEIN 6 (AHP6), a CK signaling inhibitor, up-regulated by *MP*/*ARF5* prevents CKs signaling in the border. *AHP6* moves from the peripheral zone that initiates organ primordia to the boundaries between CSR and auxin signaling-rich (ASR) region and thus, maintain a sort of two distinct hormone-based fields in the dynamic meristem developmental system [95] (Fig. 4). This suggests that the spatial position and gradient of the auxin and CKs signaling regulates the timing of organ initiation at the shoot apical meristem, A higher ratio of CKs/auxin promotes the lateral organ initiation, while a lower ratio suppress the initiation [96].

Though several genes involved in the coordination network of auxin/CKs have been identified in *Arabidopsis*, along with the genes involved in the independent auxin or CKs pathway that regulate the meristem development in grasses, the role of auxin/CKs crosstalk in the regulation of inflorescence branching in maize and rice is not yet known. The embryos of the mutants of maize type-A RR encoding gene, *aberrant phyllotaxy 1* (*abph1*), had a reduced auxin content and higher CKs levels. Higher CKs levels activate the expression of Zm*PIN1a* which promotes the expression of *abph1* through polar auxin transport. The mutant exhibits larger SAM size and altered leaf phyllotaxy. This suggests that *ABPH1-ZmPIN1a* mediated CKs-auxin crosstalk contributes to the regulation of phyllotactic patterns [97] (Fig. 3B; Supplemental table 1). In rice, overexpression of an auxin receptor encoding gene, *Auxin-signaling F-Box 6* (*OsAFB6*), increased the ratio of CKs/IAA concentration in young panicles and thus, enhanced grain yield by increasing the number of primary branches and spikelets [98]. *OsARF25*, an auxin response factor, directly binds on the promoter of *OsCKX4* and represses its expression. Overexpression and knockdown of *OsCKX4* reduces and enhances auxin biosynthesis, respectively [99]. In brief, increasing the ratio of CKs/auxin moderately during the appropriate growth stage of crop will improve grain production by increasing the number of kernels (Fig. 3D).

Meristem transition modulating the inflorescence branching in maize and rice

IM developed from SAM and BMs initiated from the IM determine the size of rice panicle or maize tassel (Fig. 1). In rice, the transition from SAM to IM is mediated by the flowering time regulation under natural short-day and long-day conditions and is very different from that in maize. The genetic interactions of QTLs

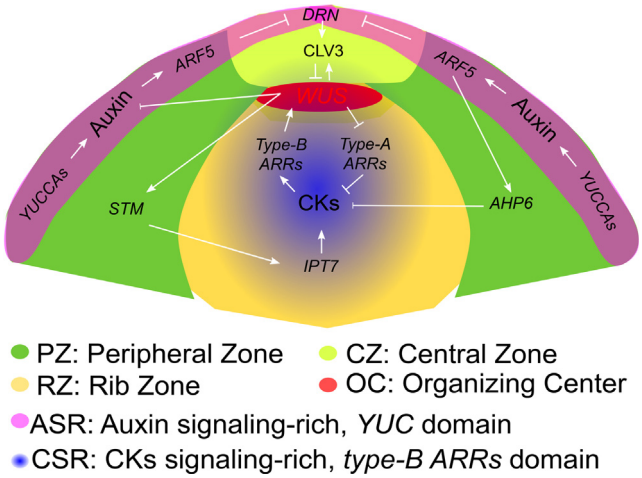

Fig. 4. Auxin-cytokinins crosstalk in shoot apical meristem of *Arabidopsis*. *WUS* represses auxin via *ARFs* and promote cytokinins (CKs) through type-A *ARRs* and *SHOOT MERISTEMLESS* (*STM*)-*ISOPENTENYLTRANSFERASE 7* (*IPT7*) pathways, respectively; while auxin and CKs activate *WUS* expression through *ARF5*- *DORNROSCHEN/ENHANCER OF SHOOT REGENERATION 1* (*DRN*) -*CLV3* and type-B *ARRs*, respectively. *ARABIDOPSIS HISTIDINE PHOSPHOTRANSFER PROTEIN 6* (*AHP6*) is a mobile signal which moves from the ASR (auxin signaling-rich) to the CSR (CKs signaling-rich) region, mediating the CKs signaling inhibition. More details are in the text.

Ghd7 (Grain number, plant height and heading date7), *Ghd8*, *Ghd7.1*/*OsPRR37*, and *Hd1* (*Heading date 1*), indicate that the number of spikelets per panicle show a positive correlation with the heading date under natural short-day conditions (Supplemental table 1). However, this correlation was observed few days before the heading under natural long-day conditions [100]. *Rice TFL1/CEN homolog* (*RCNs*) formed the florigen repression complex with 14–3-3 and OsFD1 to repress florigens activation complex by competing to florigen Hd3a for 14–3-3 binding [101] (Fig. 5; Supplemental table 1).

SMs, attached on the rice PBs and SBs, as well as on the maize ear cob, originate from IMs or BMs and then differentiate to FMs. Any disturbance in this process results in an abnormal inflorescence branching. Classical mutants with BM-SPM defects are defined as *ramosa* inflorescences in maize, such as *ramosa 1* (*ra1*), *ra2*, *ra3,* and *rel2* (*ramose enhancer locus2*) [66,102-105], which are characterized by increased number of long branches in tassel- and ear-inflorescences. Both *ra2* and *ra3,* which act upstream of *ra1* and *rel2* in parallel, enhance the activity of *ra1* and repress the determinacy of SPMs. Therefore, any double mutant with *ra1* exhibits increased long branches in the ears. *trehalose 6-phosphate phosphatase 4* (*tpp4*) mutant has a normal ear, but it enhances *ra3* ear branching, indicating its functional redundancy with its paralogue *ra3* [106]. Therefore, these genes in the RAMOSA pathway ensure the determinacy of SPMs to block the production of long branches (Fig. 5; Supplemental table 1). *BRANCHED SILKLESS1* (*BD1*) in maize [107] and its rice ortholog *FRIZZY PANICLE* (*FZP*) [108,109] also modulate the BM-SPM/BM-SM conversion. BD1/FZP is a member of AP2/ERF family of transcription factors. *bd1* and *fzp* mutants exhibit indeterminate BMs instead of SMs (Fig. 5; Supplemental table 1). Moreover, *FZP* in wheat (*WFZP*) suppresses spikelet formation, whereas its mutant produces more than one spikelet at one rachis node and forms a supernumerary spikelet-type spike architecture [110,111]. *BD1* and *FZP* are expressed at the lateral domains of the SMs of maize and rice and *WFZP* is expressed at the SMs and FMs initiation regions [107-109]. Thus, the mechanism of the transition from BMs to SMs is conserved among cereals. Delayed transition from BMs to SMs will increase inflorescence branches and result in more spikelets.

FMs, converted from SMs, produce floral organs and develop into seeds after fertilization. Maize is monoecious in which female carpels are aborted in the tassel and male stamens are arrested in the ear. This process is called sex determination, which always occurs along with inflorescence branching events and thus, share a common pathway with the determination of meristem fate [112]. Notably, *TS4* encodes a *miR172* that targets the mRNAs of *AP2*-like floral homeotic genes: *INDETERMINATE SPIKELET1* (*IDS1*) and *SISTER OF INDETERMINATE SPIKELET1* (*SID1*) [112,113] (Fig. 5; Supplemental table 1), revealing an essential role of *miR172* in the carpel arrest of maize male flower. In addition, the *miR172-IDS1* module also functions in the transition from SM to FM and is conserved in maize and rice. Rice *IDS1* (*OsIDS1*) and *SUPERNUMERARY BRACT* (*SNB*) are two orthologs of maize *IDS1* and *SID1,* respectively [114]. The double mutant *ids1;sid1* shows defective phenotypes with few branches and spikelets, extra florets in the axils of lemmas of the female floret, and indeterminate lemma-like bracts in the male floret in both rice and maize [113,114] (Fig. 5). Rice plants overexpressing *miR172* exhibit pronounced changes in the phenotype than the *snb;osids1* double mutant. Number of branches in the panicle, spikelets, and floral organs decrease remarkably in these mutants [112,115,116]. These results clearly suggest a *miR172*-mediated regulatory pathway for the inflorescence branching and spikelet meristem determinacy involving *IDS1* and *SID1/SNB* (Fig. 5; Supplemental table 1). In addition to *miR172*, *miR156* regulates the formation of BMs and SMs by targeting *SPL* genes [115] (Fig. 5). A single point mutation of *SPL14/IPA1* perturbs *OsmiR156*-directed regulation of *SPL14*, increase panicle branching and grain number, thus, creating an 'ideal plant' architecture which has a higher yield potential [73]. *miR156* gene duplication results in the formation of a mutant, *Corngrass1* (*Cg1*), which has high levels of *miR156* but low levels of *miR172* and *BD1* transcripts [117]. This results in truncation of branching steps of a normal inflorescence by bypassing SMs development and forming FMs directly from the main IM. In addition, both *FLORICAULA/LEAFY1* (*ZFL1*) and *ZFL2* in maize and *ABERRANT PANICLE ORGANIZATION* (*APO2*) in rice, which are the orthologs of *Arabidopsis LEAFY*, regulate the transition from the vegetative phase to reproductive phase [118,119]. Thereby, controlling the inflorescence architecture (Fig. 5; Supplemental table 1).

Understanding the mechanisms of inflorescence branching aid in crop breeding

Uncovering the comprehensive genetic networks associated with branching will promote the transformation of breeding strategies focused on single-locus improvement to those that focus on molecular designs based on regulatory networks. Presently, most of our knowledge about the regulation of inflorescence branching is limited to classical mutants, in which the mutations generally happened in the coding regions with knockout of gene function, resulting in inferior phenotypes. However, natural variations at non-coding regions probably contribute to the regulation of gene expression without altering the protein function, resulting in beneficial phenotypes. For instance, CNV-18 bp duplication inserted ~ 5.3 kb upstream of *FZP* repressed its expression and thus, increased the number of spikelets per panicle and enhanced grain yield by more than 15% in rice. The intergenic *KERNEL ROW NUMBER4*, ~ 60 kb downstream of *UB3* increases *UB3* expression and decreases maize kernel row number [109,120,121]. This indicates natural variations investigated for beneficial alleles can be used in breeding and fine-tuning the expression of genes required for the normal growth and development by editing their regulatory regions instead of coding region is a potential strategy to improve crop inflorescence architecture and thereby the grain yield. This strategy has been successfully used in tomato and maize.

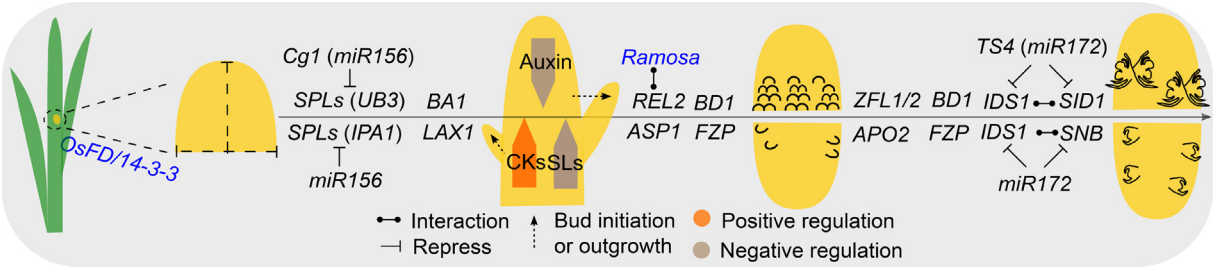

Fig. 5. Conserved networks regulating axillary meristem conversion in panicles of maize and rice. The inflorescence branching pattern is determined by meristem size, bud initiation, and outgrowth. The upper and lower panels show the conserved or stage-specific regulators that affect meristem transition in maize and rice, respectively; and the details are provided in the text. The *miR156*/*SPLs* network regulating BM-SM formation, and the *miR172* targeting ethylene response factors *IDS1* or *IDS1* and *SID1* or *SNB* pathway are highly conserved in maize and rice. However, OsFD1/14–3-3-centered florigen activation complex or florigen repression complex determining the vegetative-to-reproductive transition and RAMOSA pathway controlling SPM-SM conversion are specific in maize and rice. Importantly, auxins, transported basipetally inhibit the outgrowth of axillary buds, while cytokinins (CKs) and strigolactones (SLs) transported in the opposite direction, promote and limit the outgrowth by mitigating polar auxin transport in AMs, respectively. Genes mentioned above are also listed in Supplementary Table 1.

Rodríguez-Leal et al. used CRISPR/Cas9 driven mutagenesis of *cis*-regulatory motifs or promoters of yield trait-related genes in tomato including *SlWUS*, *SlCLV3*, *COMPOUND INFLORESCENCE,* and *SELF PRUNING* and engineered a continuum of variation in fruit size or plant branching. Liu et al. used CRISPR/Cas9 genome editing creating weak promoter alleles of *ZmCLE* genes and increased grain yields from 14 to 26% [26,122,123]. Importantly, a certain dosage of hormones, like moderate ratio of auxin/CKs level promote panicle branching and increase spikelet number [98]. Thus, fine-tuning the expression levels of the genes in the auxin and CKs biosynthesis, activation and degradation using CRISPR/Cas9 genome editing, probably improve the grain yield. Therefore, uncovering the comprehensive genetic networks associated with crop branching, followed by creating desirable alleles or genotypes by genome editing to produce optimized inflorescence architecture, will improve the grain yield. However, larger panicles and higher planting intensity in rice and maize result in lodging, dwarfism may improve lodging-resistance. Therefore, synergistically appropriate improvement of the inflorescence branches and plant heights should be achieved by crop breeding in maize and rice.

Conclusions and perspectives

Crop inflorescence branching system is complex, involving internal genes interactions, environmental interventions, and gene-environmental interactions. Here, we summarized the genetic control of inflorescence branching and grain yield in maize and rice, including the CLV-WUS feedback loop in controlling meristem size, auxin-CKs crosstalk in the regulation of axillary meristem initiation and outgrowth, the conserved *miR156*/*SPL*/*miR172* pathway, distinct rice OsFD/14-3-3 complex and maize RAMOSA networks involved in intrinsic meristem transition processes. Importantly, we suggested the creation of desirable alleles or genotypes using genome editing to fine-tune gene expressions, resulting in an ideal inflorescence architecture, which ultimately increases the crop grain yield.

However, the summary provided in this review is not comprehensive due to space limitation. In addition to auxin and CKs, other phytohormones that play key roles in controlling inflorescence branching are rarely discussed. For instance, SLs regulate the transcription of *IPA1* and *DEP1* which control rice tillering and branching [124,125]. Ethylene acts as a developmental signal and controls ear length and kernel number [126]. Further, the coordinated regulation of multiple hormones involved in inflorescence branching and thus, yield traits remain to be elucidated. Specifically, the crosstalk between stress hormones and developmental hormones in inflorescence branching needs to be established. Besides optimizing the panicle architecture, this will also help to balance the panicle branching (growth) and stress defense. Finally, the environmental cues, particularly plant density, has a huge impact on crop yield through modulating tillering and branching numbers, which are a set of adaptive responses for red and far-red light ratios [127]. In addition to light, the nutrition signals, such as inorganic nitrogen and phosphate, can act as substrates and participate in the biosynthesis of root-derived CKs and SLs. High nitrogen concentration triggers CKs transport from roots to shoots, whereas low phosphate concentration promotes SLs biosynthesis [128,129]. Nevertheless, the complex interactions among external cues, endogenous signals, and genetic factors controlling inflorescence architecture needs further exploration. Knowledge of these interactions is useful to enhance crop productivity.

Branches, including tillers or shoot branches and panicle branches, are lateral organs during the vegetative and reproductive stages in crops, respectively. Both tillers and panicle branches formation can be separated into two stages, bud formation and bud outgrowth. Therefor in few crops, these two types of branches are regulated by similar genetic mechanisms. This is observed in rice that have multiple tillers and panicle branches. For instance, both *moc1* and *lax1* mutants showed reduced number of tillers and panicle branches. However, in most crops, shoot and panicle branches are not always regulated by a similar mechanism, such as maize *TB1* and its orthologues. In maize, *TB1* controls tillers from "multiple to one" in its wild ancestor teosinte to modern maize rather than panicle branches, as well as *OsTB1*. This could be explained by the limited gene expression domain of *TB1* which is only expressed in the tiller buds and suppress tiller bud formation [130,131]. In wheat, the up-regulation of *TaTB1* expression suppresses the formation of tillers, but promotes the formation of spikelets [132]. This suggests that the same gene could have opposite effects on tillering and panicle branching. This raises a fundamental question regarding the inconsistencies in the effects of branching event-related genes on vegetative and reproductive branches. One possibility is the regulation of tillers and panicle branches is the consequence of a subset of genes that functions spatially and temporally. Apical dominance could be another hypothesis. Crops like maize and sorghum with one stalk show enhanced apical dominance and this could be controlled by *TB1* in maize; while rice, wheat, and barley have multiple tillers and therefore, weak apical dominance. This could be mediated by *OsWUS/TAB1 via* Auxin response [37]. However, the coordinated regulation of crop branch events during the vegetative and reproductive stages remains elusive. Strengthening the research on coordinated control of crop branching during these two growth stages can enrich our understanding of branching organogenesis and also contribute to creating an ideal crop plant architecture.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jare.2022.01.012.

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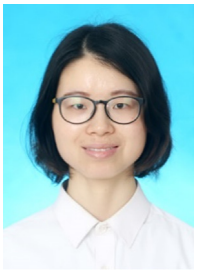

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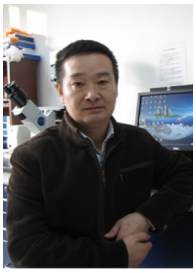

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