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REVIEW

Molecular and genetic pathways for optimizing spikelet development and grain yield

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Abstract The spikelet is a unique structure of inflorescence in grasses that generates one to many flowers depending on its determinate or indeterminate meristem activity. The growth patterns and number of spikelets, furthermore, define inflorescence architecture and yield. Therefore, understanding the molecular mechanisms underlying spikelet development and evolution are attractive to both biologists and breeders. Based on the progress in rice and maize, along with increasing numbers of genetic mutants and genome sequences from other grass families, the regulatory networks underpinning spikelet development are becoming clearer. This is particularly evident for domesticated traits in agriculture. This review focuses on recent progress on spikelet initiation, and spikelet and floret fertility, by comparing results from Arabidopsis with that of rice, sorghum, maize, barley, wheat, *Brachypodium distachyon*, and *Setaria viridis*. This progress may benefit genetic engineering and molecular breeding to enhance grain yield.

Keywords Yield improvement, Inflorescence, Spikelet, Fertility, Breeding

INTRODUCTION

The family of grasses (Poaceae) contains about 10,000 species, many of which are essential crops, including rice (*Oryza stavia*), maize (*Zea mays*), barley (*Hordeum vulgare*), wheat (*Triticum aestivum*) and sorghum (*Sorghum bicolor*). Indeed, the grains produced from these cereals are regarded as staple food and feed for humans and livestock (Kellogg 2001). Considering that the demands for grains will increase due to the projected rise in population, and to changes in our climate, research on grain yield is a pressing scientific challenge (Grierson et al. 2011).

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The architecture of the grass inflorescence determines its reproduction and yield, and is, therefore, a key agricultural trait to modify to improve yield and ease of harvesting (Doebley et al. 2006). The architecture of grass inflorescence is complex and diverse, and largely depends on the activity of the inflorescence meristem (IM; see Box 1 for explanations to all acronyms) and axillary meristem (AM) (Kellogg et al. 2013; Koppolu and Schnurbusch 2019; Zhang and Yuan 2014). Based on the lateral organ growth patterns that originate from AMs (branches and spikelets), inflorescence architectures are typically categorized as "racemes" (spikelets are pedicellate in a single central monopodial axis), "spikes" (spikelets lack pedicels, exemplified in wheat, barley and *Brachypodium distachyon*), and "panicles"

(with higher order branching, exemplified in rice and sorghum) (Fig. 1). This inflorescence definition system is borrowed from dicots (Kellogg et al. 2013). However, in contrast to the determinate growth of flowers, a spikelet contains one to many florets depending on whether the spikelet meristem (SpM) is determinate or indeterminate. Therefore, the spikelet is not equivalent to the eudicot flower, and the grass inflorescence is also named as "compound spikes" (Endress 2010). Consequently, the number, growth patterns and morphogenesis of spikelets have profound influence on grain yield potential, with key agricultural potentials in grass breeding selection.

The spikelet emerges from SpM, a specialized AM that originates from the IM and branch meristem (BM). The spikelet is enclosed by glumes, or subtended by other subsidiary organs, such as the sterile lemma in rice, and the bristle in *Setaria viridis* (Fig. 1B). Subsequently, a flower meristem (FM) arises in the spikelet to produce floral organs, which are terminated by seed growth. A spikelet contains one or multiple florets based on the timing of SpM termination. Rice and maize spikelet structures are considered typical determinate spikelets, which generate fixed numbers of florets; one floret in the rice panicle and two florets in the maize tassel (Bommert et al. 2005). Spikelets of wheat and Brachypodium are indeterminate and produce different numbers of florets, largely determined by environmental conditions (Fig. 1B). The grass floret generally consists of non-reproductive (lemma, palea and lodicule) and reproductive (stamen and pistil) organs. Because the spikelet and floret structures are obviously different in dicots and monocots, and even among grass family members, many important and sometimes controversial biological questions remain to be answered. For example, what are the driving forces behind maize and sorghum producing spikelet pairs and not single spikelets as in rice? Why do only the sessile and not the pedicellate spikelets produce perfect flowers in sorghum (Fig. 1B)? Such spikelet structures are also evident in barley, whose inflorescence forms a triplet spikelet, with the two lateral spikelets being sterile in two-rowed barley (Fig. 1B). Other major questions revolve around how we can improve spikelet fertility, and whether the regulatory frameworks of spikelet and floret formation are conserved or developed semi-independently across grass species? Notably, the spikelet of wild-type rice is determinate and produces only one fertile floret, but "two-florets spikelet" and "three-florets spikelet" mutants have been genetically selected (Ren et al. 2019, 2018; Zhang et al. 2017c). This demonstrates that the development of the sterile spikelet or floret is likely to have common genetic grounds in crop inflorescence. Deciphering the molecular regulators that control spikelet and floret fertility will no doubt be of importance for grain number and yield, as recently

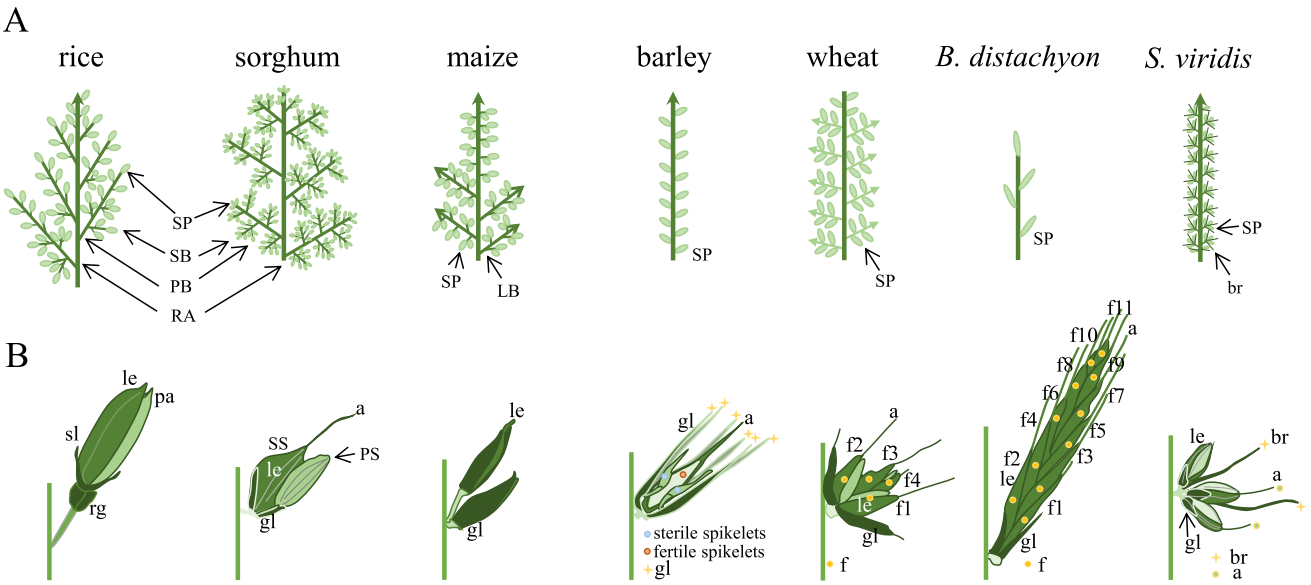

Fig. 1 Diagrams of the grass inflorescences (**A**) and spikelets (**B**). Pictograms of rice (*Oryza stavia*) and sorghum (*Sorghum bicolor*) panicle, maize (*Zea mays*) tassel, barley (*Hordeum vulgare*), wheat (*Triticum aestivum*) and *Brachypodium distachyon* spike, and *Setaria viridis* inflorescences (**A**) and spikelets (**B**). Note that the spikelet is the structural unit of grasses inflorescence, and the diverse growth patterns of the spikelets confers inflorescence complexity (see text for details). *a* awn, *br* bristle, *le* lemma, *f* flower, *gl* glume, *LB* lateral branch, *pa* palea, *PB* primary branch, *PS* pedicellate spikelet, *RA* rachis, *rg* rudimentary glume, *SB* secondary branch, *sl* sterile lemma, *SP* spikelet, *SS* sessile spikelets

exemplified in rice, sorghum, barley and wheat (Boden et al. 2015; Dampanaboina et al. 2019; Dixon et al. 2018b; Gladman et al. 2019; Jiao et al. 2018; Ren et al. 2018; Zhang et al. 2017c; Zwirek et al. 2019). There are several recent comprehensive reviews that summarize our knowledge on grass inflorescence branching and flower development (Callens et al. 2018; Gao et al. 2019; Gauley and Boden 2019; Koppolu and Schnurbusch 2019; Kyozuka 2014; Kyozuka et al. 2014; Sakuma and Schnurbusch 2020; Zhang and Yuan 2014; Zhu and Wagner 2020). In this review, we aim to summarize and synthesize current progress on molecular modules that underpin yield improvement, including spikelet initiation and floret fertility, in important grasses.

THE FLORIGEN PATHWAY DECIDES WHEN TO FLOWER AND THE NUMBER OF SPIKELETS

Similar to other AMs, the spikelet development typically involves a three-phased transition, including meristem initiation, meristem identity maintenance and termination, which is regulated by environmental and endogenous signals (Fig. 2). Hence, the timing of flowering is adjusted to environmental conditions that in turn determine the initiation of spikelets and florets. Precocious flowering generally causes a determinate inflorescence structure with less axillary organs, e.g. inflorescence branches, spikelets and flowers. In this section, we briefly highlight the mechanisms behind the decision of plants to flower and highlight potential breeding targets.

In Arabidopsis, the canonical flowering pathways promote reproductive development by activating floral pathway integrator genes, which respond to environmental conditions, such as light and temperature, and the circadian clock. Here, the *FLOWERING LOCUS T* (*FT*) is a key integrator gene of florigen, i.e. a flower-inducing molecule. *FT* may be induced by increased temperatures (Balasubramanian et al. 2006; Kim et al. 2012), and is activated directly by the photoperiodic timer gene *CONSTANS* (*CO*) under long day (LD) conditions in leaves (Imaizumi et al. 2003; Putterill et al. 1995). The FT protein can be transported through the leaf and stem vasculature to the shoot apical meristem (SAM), where it forms the "florigen activation complex" (FAC) with FLOWERING LOCUS D (FD) and 14-3-3 proteins (Andres and Coupland 2012; Song et al. 2013; Turck et al. 2008). The FAC accelerates flowering by activating the expression of the floral integrator gene *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS 1* (*SOC1*) and FM identity gene *APETALA1* (*AP1*) (Fig. 3) (Abe et al. 2005; Corbesier et al. 2007; Taoka et al. 2011; Wigge et al. 2005). Overexpression of *FT* may shorten the transition time from IM to AM, as well as antagonize functions of its homologous gene *TERMINAL FLOWER1* (*TFL1*) in IM maintenance. Indeed, increased production of TFL1

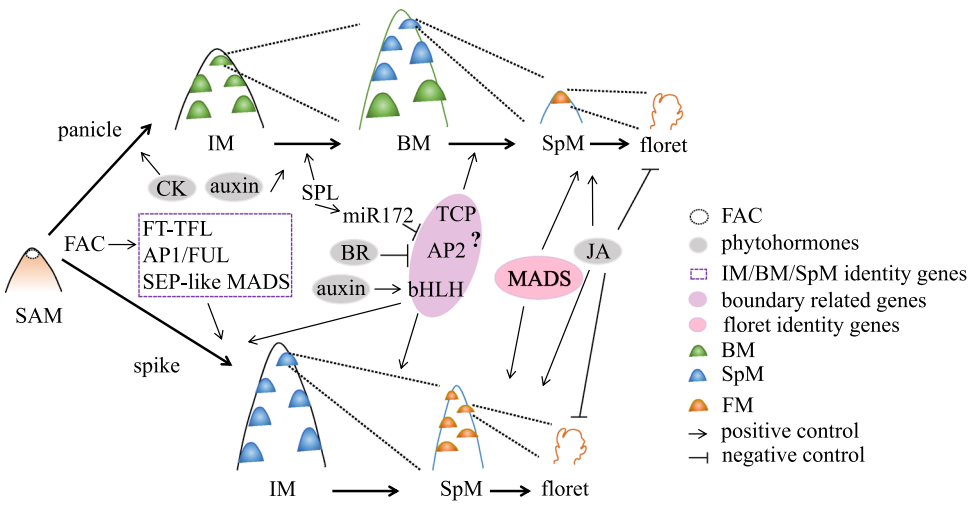

Fig. 2 Molecular modules for specifying spikelet identity and floret fertility. Spikelet arises from the spikelet meristem, which is derived from inflorescence or branch meristem. The "florigen activation complex" (FAC) complex integrates environmental and genetic signals to promoter flowering and inflorescence development. Phytohormones such as CK and auxin play important roles in maintaining meristem activity and primordium emergence. The FT-TFL, AP1/FUL and SEP-like MADS TFs interact antagonistically or in parallel with each other to establish IM and BM identity, while BR might restrain expression region of boundary genes to establish spikelet identity. Early expression of such boundary genes might confer "unbranch"-spike architecture. The phytohormone JA plays important role in floret fertility, and this pathway could be utilized in increasing floret number. *BM* branch meristem, *BR* brassinosteroid, *CK* cytokinin, *FAC* florigen activation complex, *IM* inflorescence meristem, *SpM* spikelet meristem. See also Table 1 and Box 1 for further explanations

Table 1 Transcription factor functions in spikelet initiation and development

Family	Gene function	Arabidopsis	Rice	Maize	Barley	Wheat	Sorghum
MADS	IM, SMs and FMs identity	*APETALA1* (*AP1*) (Wigge et al. 2005), *CAULIFLOWER* (*CAL*) and *FRUITFULL* (*FUL*) (Ferrandiz et al. 2000)	*OsMADS14*, *OsMADA15* and *OsMADS18* (Wu et al. 2017)	–	–	*VRN1*, *FUL1* and *FUL3* (Li et al. 2019)	–
			OsMADS1, *OsMADA5* and *OsMADS34* (Wu et al. 2018)	–	–	–	–
bHLH	AM activity	*REGULATOR OF AXILLARY MERISTEM FORMATION* (*ROX*) (Yang et al. 2012)	*LAX PANICLE1* (*LAX1*) (Tabuchi et al. 2011)	*Barren stalk1* (*ba1*) (Gallavotti et al. 2004)	–	–	–
		–	*LAX2* (Tabuchi et al. 2011)	*BA2* (Yao et al. 2019)	–	–	–
SPL	AM activity	*SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 3* (*SPL3*), *SPL9* and *SPL15* (Wang et al. 2009; Yamaguchi et al. 2009)	*OsSPL14* (Jiao et al. 2010; Miura et al. 2010; Wang et al. 2017; Zhang et al. 2017b)	–	–	*TaSPL3*, *TaSPL17* (Liu et al. 2017)	–
euAP2	Spikelet number	–	–	–	*HvAP2* (Houston et al. 2013)	*Q* (Zhang et al. 2011)	–
AP2-ERF	AM activity and SpM identity	–	*FRIZZY PANICLE* (*FZP*), *MULTI-FLORET SPIKELET1* (*MFS1*) (Bai et al. 2017; Ren et al. 2013)	*Branched silkless1* (*bd1*) (Chuck et al. 2002)	*Compositum 2* (*com2*) (Poursarebani et al. 2015)	*Branched headt-A1* (*bht-A1*) (Poursarebani et al. 2015)	–
TCP	AM activity and boundary formation	–	*OsTB1* (Lyu et al. 2020)	*TEOSINTE BRANCH1* (*TB1*) (Doebley et al. 1997)	*HvTB1*/ *INTERMEDIUM-C* (*INT-C*) (Ramsay et al. 2011)	*TaTB1* (Dixon et al. 2018b)	*MULTISEEDED 1* (*MSD1*) (Jiao et al. 2018)
		–	*OsTB2*/ *RETARDED PALEA1* (*REP1*) (Lyu et al. 2020)	*Branch angle defective1* (*bad1*)/ *Wavy auricle in blade1* (*Wab1*) (Lewis et al. 2014)	*COMPOSITUM 1* (*COM1*) (Poursarebani et al. 2020)	–	*SbWab1* (Poursarebani et al. 2020)

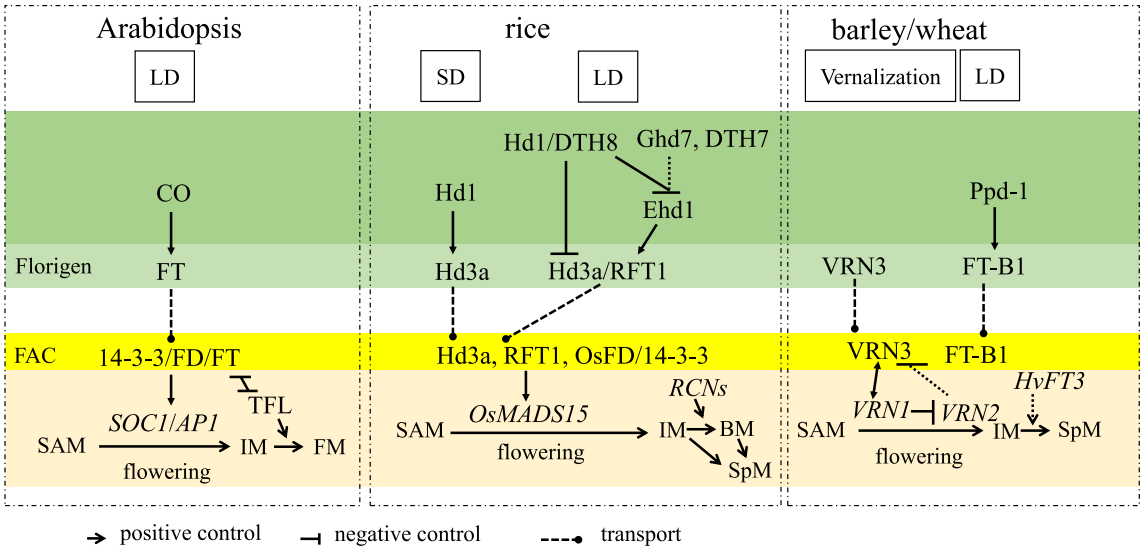

Fig. 3 Integration of environmental signals into spikelet initiation through florigen pathway. The florigen gene FT plays important role in response to environmental signals, including day length and temperature, which in turn promotes plant flowering by activating the expression of reproductive identity genes, such as MADS TFs *SOC1* and *AP1* in Arabidopsis, *OsMADS15*, *OsMADS14* and *OsMADS18* in rice, *VRN1* in wheat and barley. The nucleotide variations of genes involved in florigen pathway, such as *Hd1*, *DTH8*, *Ghd7* and *DTH7* in rice, *VRN3* and *VRN1* in wheat and barley, as well as duplication of FT family genes contribute to environmental adaptation, and could be targeted in plant breeding

results in more branches and flowers in Arabidopsis (Hanano and Goto 2011; Ho and Weigel 2014; Kardailsky et al. 1999; Kobayashi et al. 1999).

The flowering activation pathway appears to be conserved in cereals, though the functions of *FT*-like genes are diverse in reproductive development (Fig. 3). Rice is a typical short day (SD) plant and contains two complementary *FT*-like genes, *Heading-date 3a* (*Hd3a*) and *RICE FLOWERING LOCUS T1* (*RFT1*) (Komiya et al. 2008). Hd3a promotes flowering under inductive SD condition (Hayama et al. 2003; Kojima et al. 2002), while RFT1 induces flowering under LD condition (Komiya et al. 2008, 2009). Similar to Arabidopsis, the CO ortholog Heading date 1 (Hd1) activates the expression of *Hd3a* in leaves under SD condition. Once the FAC complex (Hd3a/RFT1-OsFD-14-3-3) is formed in the rice SAM (Tamaki et al. 2007; Taoka et al. 2011), it induces the TF *OsMADS15* by directly binding its promoter, and also alters the expression of two other flowering-promoting *AP1*/*FRUITFULL*(*FUL*)-like TFs, *OsMADS14* and *OsMADS18* (Tamaki et al. 2015). However, under LD condition, Hd1 typically represses the expression of *Hd3a* and *RFT1*, though this depends on the TF *DAYS TO HEADING 8* (*DTH8*) (Du et al. 2017; Zhu et al. 2017). The expression of *Hd3a* and *RFT1* are instead activated by the rice specific gene, *EARLY HEADING DATE 1* (*Ehd1*) under LD condition (Itoh et al. 2010). Furthermore, the expression of *Ehd1* is negatively regulated by a group of flowering repressors, including *GRAIN, PLANT HEIGHT and HEADING DATE 7* (*Ghd7*), *DTH7* (*Ghd7.1/OsPRR37*) and *DTH8* (*Ghd8*) (Fig. 3) (Wei et al. 2010; Xue et al. 2008; Yan et al. 2011, 2013). This repressor-Ehd1-florigen pathway, which modulates flowering under LD condition, is vital to adaptation to high-latitude regions (Komiya et al. 2009; Zhao et al. 2015), and natural variations in these genes impact spikelet number and yield (Gao et al. 2014; Yan et al. 2011, 2013). Genetic and molecular studies in rice have repeatedly shown that the heading date is positively correlated with grain yield due to a modified transition from vegetative development to inflorescence differentiation (Liu et al. 2020). Hence, the repressor genes offer interesting breeding targets to change flowering in rice. Indeed, association analysis between *Hd1* nucleotide polymorphism and yield/quality variation in 123 major rice varieties, cultivated in China, revealed that haplotypes of *Hd1* could be utilized to improve yield of *japonica* varieties in the southern areas of China by increasing secondary branch number, grain number per plant and grain weight per single panicle (Leng et al. 2020).

Wheat and barley genomes contain at least 12 *FT* homologs, with multiple roles in plant development (Dixon et al. 2018a; Halliwell et al. 2016). This might indicate that the expansion of the *FT*-like genes family has a close connection to domestication. Similar to Arabidopsis and rice, the *FT* ortholog *VERNALIZATION3* (*VRN3*, also referred to as *HvFT1* in barley and *TaFT* in wheat) stimulates flowering by activating the expression of *VRN1* (*AP1/FUL* ortholog) in response to

vernalization (Yan et al. 2006). This transition was further enhanced by VRN3 directly repressing the expression of the negative regulator *VRN2* (Ghd7 homolog, Fig. 3) (Deng et al. 2015). It is noteworthy that the expression of *VRN3* is low before vernalization, independently of the photoperiod, but is induced by LD condition after vernalization (Hemming et al. 2008; Yan et al. 2006). Furthermore, another barley FT homolog, *HvFT3*, can control spikelet initiation independently of the photoperiod (Mulki et al. 2018). These data indicate sub-functionalization of *FT*-related genes in barley. In contrast, a wheat *FT*-like gene, *FT-B1*, is sensitive to the photoperiod. Mutations, or decreased expression, of this gene extended the time of reproductive developmental transition, resulting in increased numbers of spikelets or paired spikelets (Dixon et al. 2018a; Finnegan et al. 2018). The expression of *FT-B1* is regulated by the photo-sensitive gene *Photoperiod-1* (*Ppd-1*), an important regulator of inflorescence architecture and paired spikelet development in wheat (Boden et al. 2015), corroborating that expression of flowering genes could be fine-tuned to increase the number of spikelets and modulate wheat inflorescence architecture.

From the above, it is clear that although the FT pathway differs in different plants, it accelerates flowering in most of them (Putterill and Varkonyi-Gasic 2016). However, there are exceptions to this rule as the FT-like gene *BvFT1* represses flowering in sugar beet (Pin et al. 2010). In addition, the *FT* homolog, *MOTHER OF FT AND TFL1* (*MFT*), plays only a minor role in Arabidopsis flowering (Yoo et al. 2004). A recent study in rice found that the *FT*-related gene, *OsMFT1*, may repress the expression of the APETALA2/ETHYLENE RESPONSE FACTOR (AP2/ERF) TF *FRIZZY PANICLE* (*FZP*) and *SEPALLATA* (*SEP*)-like genes, which in turn regulate heading date and panicle structure. As a consequence, overexpression of *OsMFT1* prolonged the transition from BM to SpM to produce more branches and spikelets (Song et al. 2018).

The interactions between florigen *FT* and the antagonistic "anti-florigen" *TFL1*-like genes are not well studied in grasses yet, but the *TFL1* pathway is conserved among Arabidopsis, rice and maize in regulating inflorescence architecture. Here, reduced expression of *TFL1* homologs, *RICE CENTRORADIALIS 1–4* (*RCN 1–RCN 4*), produced small panicles, while overexpression of *RCN1*, *RCN2* or *RCN4* led to increased branching due to the delay of transition to the reproductive phase (Liu et al. 2013; Nakagawa et al. 2002). In maize, ectopic expression of the *TFL1*-like genes can also modify flowering time and inflorescence architecture (Danilevskaya et al. 2010), but the downstream components of the *TFL1* pathway in crop inflorescence development and spikelet initiation need to be clarified. Nevertheless, these results indicate that florigen pathway is not only controlling flowering time and its adaption, but also has a prominent role in determining spikelet number and yield selection (Figs. 2, 3).

Optimal seasonal timing of flowering is one of the most important breeding targets as it is essential in adapting cereal crops to temperate climates, and for grain production. Molecular marker-assisted selection has resulted in an increased number of haplotypes and alleles in flowering genes in cereals (Hickey et al. 2019). On the molecular level, CRISPR/Cas9 genome editing systems may further aid in generating many new alleles (Chen et al. 2019; Rodriguez-Leal et al. 2017). For example, such approach may enable fine-tuning the expression of flowering repressors, such as *DTH8*, *Ghd7*, *DTH7* in rice and *VRN2* in wheat and barley, which could boost branching to increase the number of spikelets. On the other hand, enhanced activity of the anti-florigen *TFL*-like genes might also promote higher-order branching of inflorescence and increase yield, and thus become suitable breeding targets.

PHYTOHORMONE GRADIENTS DETERMINE SPIKELET INITIATION AND OUTGROWTH

Once an Arabidopsis plant is dedicated to flowering, spatial and temporal distribution of phytohormones, including auxin, cytokinin (CK), brassinosteroids (BRs) and gibberellic acids (GAs), trigger FM initiation and outgrowth (Wils and Kaufmann 2017). In this section, we briefly outline how hormone distributions and components influence inflorescence development.

Auxin is a morphogen that determines almost every aspect of plant growth and development (Zhao 2018). In Arabidopsis inflorescence development, the activity of auxin efflux transporter *PIN-FORMED 1* (*PIN1*) produces an auxin maxima, which determines the site of floral primordium by activating the expression of auxin responsive gene *AUXIN RESPONSE FACTOR* 5/*MONOPTEROS* (*ARF5*/*MP*) (Okada et al. 1991; Yamaguchi et al. 2013). ARF5/MP then directly activates the expression of FM identity genes, such as *LFY* and *AINTEGUMENTA* (*ANT*), by recruiting SWI/SNF chromatin remodeling complexes RAHMA (BRM) and SPLAYED (SYD) to increase accessibility of the DNA for the induction of key regulators of flower primordium initiation (Wu et al. 2015; Yamaguchi et al. 2013). Then *LFY*, *ANT* and other transcription factors (TFs), including *AP1-CAULIFLOWER* (*CAL*)-*FRUITFULL* (*FUL*) (discussed below), form feed-forward and feed-back loops to establish FM identity (Liu and Mara 2010).

Auxin maxima also determine the site and initiation of spikelet in grasses. In maize, mutations in genes related to auxin biosynthesis or polar auxin transport, such as *SPARSE INFLORESCENCE1* (*SPI1*, an ortholog of *YUCCA* that regulates auxin biosynthesis), *ZmAux1* (an auxin influx transporter) and *BARREN INFLORESCENCE2* (*BIF2*, an ortholog of *PINOID*), led to barren inflorescence and/or less spikelets (Gallavotti et al. 2008a, b; Huang et al. 2017). Similar phenotypes were also observed in *Setaria viridis*, where the inflorescence of a *SvAUX1* mutant contained less branches than that of wild type (Huang et al. 2017). Although there is no direct genetic evidence for a role of auxin in rice inflorescence development, auxin maxima were observed during IM progression using the auxin biosensor markers *DR5rev*-VENUS and *DII-VENUS* (Yang et al. 2017). It is plausible that gene redundancy of certain auxin biosynthesis, transport or response genes might mask the impact of the auxin pathway in rice spikelet initiation.

CK controls many processes in plant growth and development, including cell proliferation and differentiation, shoot and root architecture, light and stress responses and senescence (Hwang et al. 2012). In Arabidopsis, high concentrations of CK promote AM initiation in shoot regeneration and the leaf axils by activating expression of meristem marker gene *WUSCHEL* (*WUS*) (Zhang et al. 2017a, d). However, it is unclear if CK also drives *WUS* expression during FM formation. Nevertheless, AP1 does repress CK accumulation in the axil of sepals to inhibit secondary floret growth by suppressing the cytokinin biosynthetic gene *LONELY GUY1* (*LOG*) and activating the cytokinin degradation gene *CYTOKININ OXIDASE/DEHYDROGENASE3* (*CKX3*) (Han et al. 2014). These results indicate that high content of CK correlates with strong meristem activity in Arabidopsis. In rice, increased levels of CK result in a boost in spikelet numbers and in yield. Indeed, the CK degrading enzyme *cytokinin oxidase/dehydrogenase* (*OsCKX2*) has been one of the main yield breeding loci during rice domestication (Ashikari et al. 2005; Kurakawa et al. 2007; Li et al. 2013). In contrast to Arabidopsis, blocking CK signal transduction decreases IM activity in rice (Worthen et al. 2019), implying that distinct pathways might control inflorescence development in grasses. Consistent with this hypothesis, multiple genes involved in CK biosynthesis, degradation and signaling regulate cereal inflorescence development (Chen et al. 2020; Yamburenko et al. 2017). In addition, CK concentration is increasing in an apical-to-basal pattern, which is opposite to the auxin gradient and to the expression pattern of *Six-rowed spike 2* (*Vrs2*), encoding a SHORT INTERNODES (SHI) TF in floral organ patterning (Youssef et al. 2017), during early barley inflorescence development. This indicates that hormone gradients might play a pivotal role in balancing meristem activity and organ outgrowth. However, detailed functions of these distribution patterns in spikelet initiation, fertility and growth duration are still underappreciated.

BRs are a group of steroid hormones known for their function in cell elongation and stress response. The spatial and temporal distribution patterns of BRs affect inflorescence and flower development (Li and He 2020). Several studies in Arabidopsis found that organ boundary formation was altered in BR deficient and constitutive mutants. For example, the BR responsive TFs BRASSINAZOLE RESISTANT 1 (BZR1) and BR1-EMS-SUPPRESSSOR 1 (BES1) could recruit the general repressor TOPLESS (TPL) to repress the expression of boundary identity genes *CUP SHAPED COTYLEDON 1* (*CUC1*), *CUC2*, *CUC3*, *LATERAL ORGAN FUSION1* and *LATERAL ORGAN BOUNDARIES* (*LOB*) (Gendron et al. 2012). Moreover, LOB activated the expression of *PHYB ACTIVATION TAGGED SUPPRESSOR1* (*BAS1*), a cytochrome P450 enzyme that inactivates BRs, to form a negative feed-back loop and limit growth in boundary regions (Bell et al. 2012). Consistent with BRs role as a positional cue, clustered inflorescence and paired spikelets were observed in rice BR-deficient mutant *panicle morphology mutant 1* (*pmm1*) (Li et al. 2018). In addition, the number of spikelets was changed in BR biosynthesis and signaling transduction mutants, such as *dwarf 11* (*d11*) alleles (Wu et al. 2016; Zhou et al. 2017), and *bri1-associated receptor kinase* (*Osbak1*)/*Ossg2* (Yuan et al. 2017). In some *aus* rice varieties, two copies of the CGTG motifs, i.e. an OsBZR1 binding motif, are present in the promoter of *FZP*, which resulted in repression of *FZP* and in increased number of spikelets due to a longer transition of SpM to FM identity (Bai et al. 2017). Therefore, the numbers of CGTG motifs in the *FZP* promoter could be targeted in rice breeding efforts. Whether the BZR1-FZP regulatory module is conserved also in other grasses is an interesting question that remains to be addressed.

In Arabidopsis, the FM identity component LFY can suppress the content of GA, a group of tetracyclic diterpenoid hormones that modulate cell division and elongation (Xu et al. 2014). LFY may here activate the expression of *EUI-LIKE P450 A1* (*ELA1*), encoding a P450 enzyme that catabolize bioactive GAs (Yamaguchi et al. 2014). In parallel, the levels of DELLAs (repressors of GA signaling pathway) increase and interact with SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 9 (SPL9), which then activate the expression of *AP1* to enforce FM identity (Yamaguchi et al. 2014; Yu et al.

2012). Furthermore, studies in Arabidopsis and barley found that accumulation of DELLAs limits IM size (Serrano-Mislata et al. 2017), indicating that the spatio-temporal GA distribution affects the number and onset of flowers that in turn contribute to yield. Indeed, a longitudinal inflorescence GA gradient regulates patterning in barley (Youssef et al. 2017). However, whether such gradients, and the corresponding upstream regulatory loop, i.e. LFY-ELA1-SPL9-AP1 in Arabidopsis, plays similar roles in grass spikelet and floret initiation in other grasses remain elusive.

To summarize, we conclude that auxin plays an important and conserved function in AM initiation, while CK and BR appear to have distinct roles in meristem transition of cereal inflorescence. For breeding applications, it will be crucial to further explore the spatio-temporal distribution patterns of phytohormones, as well as their downstream targets, during the reproductive meristem transition of the inflorescence. Here, it seems that controlling the CK and BR levels/activity before FM initiation may contribute a key factor in increasing the number of spikelets and thus yield.

MULTIPLE TRANSCRIPTION FACTORS FUNCTION SYNERGISTICALLY IN SPECIFYING THE IDENTITY AND DEVELOPMENT OF SPIKELETS

Many TFs regulate inflorescence development. These TFs are typically directed by environmental and hormonal interactions to regulate SpM and FM identity, fertility and determinacy. These TFs typically include members of the MADS, AP2/ERF, SPL, basic helix–loop–helix (bHLH), and Teosinte branched/Cycloidea/PCF (TCP) families (Fig. 2). The TFs may interact with each other to form regulatory complexes that promote or maintain SpM identity by feed-forward or feed-back loops to guarantee the progression of spikelet and floret development (Liu and Mara 2010; Zhu and Wagner 2020). Here, we focus on select recent TF inflorescence studies and discuss how insights from these studies may guide breeding efforts.

The AP1/CAL/FUL TFs respond to FT to promote meristem transition

AP1, *CAULIFLOWER* (*CAL*) and *FRUITFULL* (*FUL*) are MIKC-type MADS-box TFs that play a critical role in FM identity and are activated by the florigen pathway in Arabidopsis. The inflorescence of *ap1 cal ful* triple mutant display leafy shoots instead of flowers (Ferrandiz et al. 2000). In rice, the inflorescence of *osmads14 osmads15* double mutant plants also produced leaf-like structures (Wu et al. 2017). Furthermore, by suppressing the expression of *OsMADS14*, *OsMADS15* and *OsMADS18* in an *osmads34/pap2* (*panicle phytomer 2*, one of *SEP*-like MADS TFs) mutant background, rice plants formed vegetative tillers on branches other than the primary ones (Kobayashi et al. 2012). Similar phenotypes were observed in the triple *SEP*-like mutant *osmads1-z osmads5-3 osmads34-1* (Wu et al. 2018), indicating that the AP1/FUL and SEP-like MADS box genes have similar roles in maintaining AM identity during reproductive development in Arabidopsis and rice. In wheat, the MADS box TFs *VRN1*, *FUL1* and *FUL3* (homologs to the AP1/FUL and SEP-like MADS box TFs above) have redundant roles in promoting spikelet initiation and spike determinacy, as well as in flowering and stem elongation (Li et al. 2019). The number of wheat spikelets increased in both *vrn1* and *ful2* single mutant, but, perhaps more interestingly, floret numbers increased in *ful2* spikelets (Li et al. 2019). Since molecular data show that the *AP1/FUL* genes can interact with different MADS-box proteins (Li et al. 2019; Wu et al. 2017), it is reasonable to deduce that many of them contribute to IM, SpMs and FMs identity determination.

The bHLH TFs respond to auxin to regulate AM initiation

In Arabidopsis, *REGULATOR OF AXILLARY MERISTEM FORMATION* (*ROX*) encodes a non-canonical bHLH protein that regulates vegetative AM activity (Yang et al. 2012). In maize, the *barren stalk1* (*ba1*) mutant, which corresponds to a mutation in the maize ROX ortholog, grows unbranched tassels with no spikelet initiation (Gallavotti et al. 2004), indicating that reproductive AM activity may be directed by different regulatory networks in plants. The rice ba1 ortholog, LAX PANICLE1 (LAX1), likewise controls spikelet initiation, and does this by interacting with LAX2 (Tabuchi et al. 2011). This is consistent with data from maize, in which the ortholog of LAX2, BA2, could interact with BA1 to regulate both vegetative and reproductive AM formation (Yao et al. 2019). Bioinformatic analyses further found that LAX2/BA2 has orthologs in Brachypodium and sorghum, perhaps indicating that the LAX1–LAX2/BA1–BA2 pathway is conserved among grasses. Based on the expression pattern of *BA2*, combined with genetic data of *ba1* and other barren inflorescence mutants (Yao et al. 2019), the BA1–BA2 pathway might function downstream of auxin signaling to position boundary regions for AM formation. Therefore, it would be interesting to study the spatio-temporal expression patterns,

and interactions, among the AP2 and bHLH boundary marker genes and proteins.

The age pathway drives a phase transition to activate spikelet initiation

In Arabidopsis, the so-called "age pathway" controls, in parallel to environmental and phytohormonal cues, the transition of vegetative-to-reproductive phase and is mediated by the miRNA156-SPL module (Yu et al. 2015). The expression of miRNA156 declines as plant ages and targets for example the TFs *SPL3*, *SPL9* and *SPL15* to promote flowering, as they activate *AP1*, *FUL* and *SOC1* (Wang et al. 2009; Yamaguchi et al. 2009). The SPL family members also play important roles in balancing plant vegetative and reproductive growth (Wang and Wang 2015). In rice, the *OsSPL14* expression correlates with the number of spikelets (Jiao et al. 2010; Miura et al. 2010; Wang et al. 2017; Zhang et al. 2017b). In switchgrass (*Panicum virgatum* L.), *PvSPL7* and *PvSPL8* induced flowering by directly activating the flower identity genes, *PvSEPALLATA3* (*PvSEP3*) and *PvMADS32*. Consistent with this observation, down-regulation of *PvSPL7* and *PvSPL8* induced inflorescence reversion (Gou et al. 2019), indicating that SPL TFs have conserved roles in promoting the transition from vegetative to reproductive growth in grasses. Such role would suggest that they also might engage with *LFY*; however, such relationships are unknown and will be exciting avenues to explore in the future.

Another aspect of the SPLs in grasses is that PvSPL4 regulates aerial axillary bud formation in switchgrass (Gou et al. 2017). Analogously, OsSPL7 binds directly to the promoter of *OsGH3.8*, one of the acyl-acid-amido synthetases in auxin catabolism, to regulate tiller number in rice (Dai et al. 2018). A recent study, furthermore, found that TaSPL3 and TaSPL17 interact with the strigolactone (SL) signaling repressor DWARF53 (TaD53) to regulate the expression of *TEOSINTE BRANCHED1* (*TaTB1*) and *BARREN STALK1* (*TaBA1*) to control tillering and spikelet development in wheat (Liu et al. 2017). Hence, the SPL family members control a variety of important inflorescence pathways in grasses.

The miRNA172–euAP2 pathway functions downstream of miRNA156-SPL module in juvenile-to-adult phase transition. In Arabidopsis, the expression level of miRNA172 is activated by SPL9 and the expression increases with age (Wu et al. 2009). Specific alleles of the euAP2 genes, a subfamily of AP2/ERF with a miRNA172-binding site, such as *Q* in wheat (Zhang et al. 2011) and *HvAP2* in barley (Houston et al. 2013), have been selected for high density of spikelets during breeding. These alleles have altered the binding site of miRNA172, rendering elevated levels of euAP2 proteins, which extended the transition duration for spikelet development to increase yield (Houston et al. 2013; Liu et al. 2018).

The AP2/ERF TFs regulate boundary formation and specify spikelet identity

The AP2/ERF family members impact stress responses and plant development; processes that control AM activity and SpM identity via hormone signaling (Chandler 2018; Zhu and Wagner 2020). An increase in floret number is associated with decreased expression of certain members of the AP2 TFs, such as *branched silkless1* (*bd1*) in maize (Chuck et al. 2002), *MORE SPIKELETS 1* (*MOS1*) in Brachypodium (Derbyshire and Byrne 2013), *FZP* and *MULTI-FLORET SPIKELET1* (*MFS1*) in rice (Bai et al. 2017; Ren et al. 2013), *compositum 2* (*com2*) in barley and *branched headt-A1* (*bht-A1*) in wheat (Poursarebani et al. 2015). Notably, the *bd1* genes are expressed specifically in the boundary region between the indeterminate meristem and differentiating lateral organ (Chuck et al. 2002; Komatsu et al. 2003), and OsBZR1 binds directly to the promoter of *FZP* (Bai et al. 2017). Therefore, as also discussed above, it would be interesting to investigate whether the AP2/ERFs contribute to a conserved boundary-establishment pathway in the inflorescence, perhaps linked to BR signaling. Understanding how AP2/ERF TFs control the fate of the SpM, both at transcriptional and translational levels, is an attractive goal and some of these TFs may be targets for cereal breeding. Potential genetic interactions between AP2/ERF and MADS TFs in grasses are also awaiting to be uncovered.

The TCP TFs promote boundary formation

TEOSINTE BRANCH1 (TB1) encodes TCP protein (named after TB1 in maize, CYC in *Antirrhinum majus* and the proliferating cell factor DNA-binding proteins of rice), a gene first cloned in maize where it regulates tillering and ear size as one of the genetic loci for maize domestication (Doebley et al. 1997). In Arabidopsis, rice and barely, the role of *TB1* orthologs in repressing axillary bud outgrowth is well studied (Wang et al. 2018). However, the TB1s role in reproductive AM development is less well understood. In wheat, TaTB1 interacts with TaFT1 to regulate axillary spikelet development and tiller number in a dosage-dependent manner (Dixon et al. 2018b). But unlike *TB1*, *OsTB1* was apparently not selected for during domestication. Certain alleles of the *OsTB1* homolog, *OsTB2*/*RETARDED PALEA1* (*REP1*), were selected for during upland rice

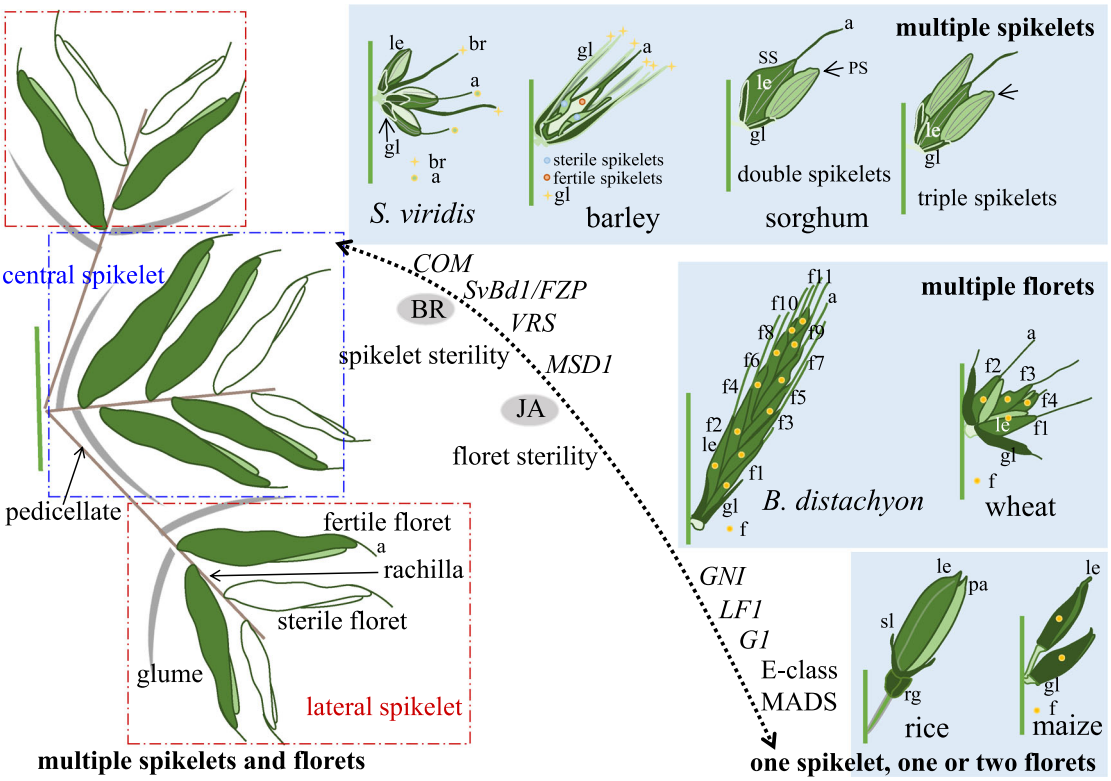

Fig. 4 A hypothetical model to modify grass spikelet structures. In cereals, the spikelet structure unit contains one to three spikelets, where the lateral one is sterile in barley and sorghum. In Brachypodium and wheat, one spikelet contains many florets, whose fertility can be converted for high yield breeding. Phytohormones (BR, JA), TCP (*COM*, *MSD1*), AP2 (*SvBd1*, *FZP*), HD-Zip (*LF1*, *VRS1*, *GNI*) TFs are involved in specifying SpM identity and fertility. Manipulation of these regulatory modules to increase spikelet number and floret fertility provides a chance to generate optimal inflorescence and spikelet architecture to improve yield. *a* awn, *br* bristle, *le* lemma, *f* flower, *gl* glume, *LB* lateral branch, *pa* palea, *PB* primary branch, *PS* pedicellate spikelet, *RA* rachis, *rg* rudimentary glume, *SB* secondary branch, *sl* sterile lemma, *SP* spikelet, *SS* sessile spikelets

adaptation, and counteract the inhibitory effect of *OsTB1* on tillering (Lyu et al. 2020). Here, *REP1* is expressed in the adaxial side of the spikelet, a boundary region between IM and SpM, where palea develops. In *rep1* mutants, palea development was retarded and cell differentiation was abnormal with less body structure of palea (Yuan et al. 2009). Therefore, sub- and/or neo-functionalization appears to have occurred in the TCP family during evolution. In sorghum, *MULTISEEDED 1* (*MSD1*) belongs to the CYC/TB1 subgroup that promotes JA biosynthesis to repress carpel fertility of pedicellate spikelets (PSs) (Jiao et al. 2018). This function is conserved in barley, where the *HvTB1*/*INTERMEDIUM-C* (*INT-C*) represses carpel fertility of lateral spikelets (Ramsay et al. 2011). The *OsTB2*/*REP1* homologous gene *COMPOSITUM 1* (*COM1*) is expressed specifically in barley inflorescence meristem boundaries, and the *com1* mutant grew branch-like structures instead of floret, indicating that *COM1* confers SpM identity (Poursarebani et al. 2020). In maize, *branch angle defective1* (*bad1*)/*Wavy auricle in blade1* (*Wab1*), homolog of *COM1* and *OsTB2*/*REP1*, expresses specifically in the axil of branches, spikelet pair meristems and branch meristems of tassel (Lewis et al. 2014). Furthermore, mutations of *SbWab1*, TCP homologous in sorghum, caused the plants to grow upright tassel branches and reduced the number of primary inflorescence branches (Poursarebani et al. 2020). Therefore, genes duplicated in the grass CYC/TB1 family might be recruited independently to regulate inflorescence development and contribute to inflorescence branching, SpM identity and carpel fertility, depending on their interactions with other TFs.

Since multiple TFs (Table 1), such as *OsSPL14* and *FZP* in rice, *TB1* in maize, *Q* in wheat, *INT-C* in barley have been selected for high-yield breeding during domestication (see above), a rational design to create defined ideotypes was proposed as future breeding strategies (Qian et al. 2016). Due to the distinct inflorescence architecture in cereal plants, the basic scheme behind such rational design is to balance the number of branches and spikelets to promote maximum yield. Since the expression dosage and patterns of SPL-AP2 and TCP TFs play essential roles in inflorescence

branching and the number of spikelets, their genome duplication and regulatory modules are worth further investigation to optimize yield. As exemplified in tomato breeding, combining different natural alleles in MADS TF *SEP4* genes with gene-editing techniques could modulate inflorescence complexity and improve yield (Soyk et al. 2017). Therefore, comparative genomic studies of TFs across different cereals would not only enhance our understanding of inflorescence development but also open a window for rational breeding.

HIGH YIELD BREEDING: IMPROVING THE NUMBER AND FERTILITY OF SPIKELETS AND FLORETS

Increasing the number and size of spikelets are main strategies for high-yield breeding. Based on mutant screening and functional genetic analyses of rice *long sterile lemma* (*G1*) and *LATERAL FLORET 1* (*LF1*), the three-florets-spikelet model was indicated as a probable ancient rice spikelet structure (Yoshida et al. 2009; Zhang et al. 2017c). This observation led to new breeding strategies for multiple-florets spikelet selection (Ren et al. 2020). With more comparative data from other grass plants, we propose that the grass spikelets could be modified from a spikelet containing one floret to a compound spikelet with multiple spikelets and many florets by modifying different molecular modules that function in releasing space constraint, and improving spikelet and floret fertility (Fig. 4).

As indicated above, the structure of the grass spikelets is quite diverse, depending on the fertility of lateral spikelet or floret. Notably, it appears that the spikelet and floret fertility was lost independently several times in different cereal plants during adaptation and domestication (Sakuma and Schnurbusch 2020). The *S. viridis*, two-rowed barley and sorghum belong to the multiple spikelets group, where three or two spikelets grow in a structural unit. However, the lateral spikelets are sterile in two-rowed barley and sorghum, whereas a bristle structure accompanies spikelet development in *S. viridis* (Figs. 1B, 4). Recent work in the *S. viridis d11* mutant, called *bristleless1* (*bsl1*), found that BR levels specify bristle identity and maintain the SpM activity (Yang et al. 2018). *Bsl1* expression was detected at the base of secondary and higher order axillary branches, as well as the initiation sites of lateral spikelet organ. In the *bsl1-1* mutant, the boundary gene *SvBd1* was ectopically expressed in the developing spikelet (Yang et al. 2018), suggesting that *Bd1* class AP2 TFs plays a conserved role in establishing boundary and specifying SpM identity. Therefore, by reducing the BR levels or extending the expression of AP2-type boundary genes during meristem transition, one could generate multiple spikelets in *S. viridis*. In fact, this strategy was already adopted in 17 accessions in the *aus* subpopulation of rice, yielding increased spikelets per panicle (Bai et al. 2017). Hence, modulating the BR levels in the boundary region could be a potential way to alter yields.

Studies on mutants with fertile lateral spikelets revealed that a group of *Vrs* TFs confer lateral spikelet sterility in barley, making the *vrs1* a key genetic locus to change lateral spikelet fertility (Zwirek et al. 2019). *Vrs1* belongs to the homeodomain leucine zipper I class (HD-Zip I) TFs, and is expressed mainly in the lateral spikelet and inhibits female organ development (Komatsuda et al. 2007; Sakuma et al. 2013). The expression of the *Vrs1* ortholog in wheat, *Grain Number Increase 1-A* (*GNI-A1*), was detected in the most apical floret primordia, and its expression correlated with floret sterility (Golan et al. 2019; Sakuma et al. 2019). These data indicate that during domestication, Vrs1/GNI-A1 was a key locus for selection in high-yield breeding. Therefore, developing an appropriate number of floret primordia would be helpful to improve grain numbers. Optimizing the functionality of HD-Zip I and AP2 TFs may similarly help improve floret fertility and number, though detailed studies of many of these are lacking.

In the rice *lateral floret1* (*lf1*) mutant, a single T to C substitution in the binding site of *miRNA165/166* increased the expression level of *LF1*, which encodes an HD-Zip III TF, and led to activation of meristem marker gene *OSH1* in the axillary side of sterile lemma to produce more florets in a spikelet (Zhang et al. 2017c). Hence, the HD-Zip I and III TFs might play antagonistic roles in maintaining FM activity. How this relationship was established in grasses remains an open question, but may also become a relevant target to change reproductive development.

In sorghum, JA content is correlated with carpel fertility. Inflorescence of sorghum generates two kinds of spikelet, sessile spikelets (SSs) and PSs, and only SSs develop normally to set grain, while growth of PSs is aborted without carpel (Figs. 1B, 4). Mutant screening of fertile PSs identified three genes, *MULTISEEDED 1* (*MSD1*), *MSD2* and *MSD3* (Dampanaboina et al. 2019; Gladman et al. 2019; Jiao et al. 2018). *MSD1* encodes a TCP TF that binds to the promoter of *MSD2*, which encodes a lipoxygenase (*LOX*) in the JA biosynthesis pathway (Gladman et al. 2019; Jiao et al. 2018). *MSD3* is an ortholog of Arabidopsis *FATTY ACID DESATURASE 7* (*FAD7*), another enzyme involved in JA biosynthesis (Dampanaboina et al. 2019). Although it is still not clear why high JA concentration triggers programmed cell

death of SPs, similar to one of the sex-determining pathways reported in maize tassel development (Acosta et al. 2009), the function of JA in FM activity seems conserved in grasses. The JA content also impact organ development and seed numbers in sorghum, maize and rice mutants, i.e. reduced JA content led to less seed setting but new flower organs (Acosta et al. 2009; Cai et al. 2014; Jiao et al. 2018; Li et al. 2009; Ren et al. 2018). Furthermore, genetic and molecular studies revealed that the JA responsive TF OsMYC2 binds to the promoter of FM identity gene *OsMADS1* to promote meristem identity transition from SpM to FM during rice inflorescence development (Cai et al. 2014; You et al. 2019). OsMADS1 is one of the SEP-like MADS box TFs that confers floral organ identity and maintains FM activity (Hu et al. 2015). Therefore, the spatiotemporal distribution of JAs plays many roles in regulating plant reproductive organ development. Although the distribution pattern of JAs in spikelet development is unclear, it may be attractive to harness the pathway that modulates JA content to increase floret fertility.

CONCLUSIONS

In summary, even though there are some species specific networks that promote flowering, activate spikelet development and increase spikelet fertility, some common regulatory modules certainly exist among cereals. Increasing numbers of studies in the different grass species will improve on similarities and differences in these pathways and modules. Manipulation of the key regulatory modules, such as flowering time, controlled by the FAC-AP1/FUL module, spikelet number, regulated by the SPL-miRNA172-AP2 and BR-FZP modules, and floret fertility, managed by TFs-phytohormone modules, provides many opportunities to enhance inflorescence and spikelet architecture to improve yield.

To improve grain yield, modulating floret fertility by reducing floret abortion are representing a promising breeding strategy in wheat and other plants without branched spikes. Similarly, increasing floret number per spikelet is another strategy in rice and plants whose FM is determinate. However, both these strategies have space constraints (Fig. 4). A 'compound spikelet' with multiple spikelets and florets would need more "growth space" as well as nutrient supplements, which depends not only on genetic regulators in spike branching, and on spikelet and floret fertility, but also on developing an appropriate system to balance resistance and growth.

Abbreviations

AM	Axillary meristem
AP2/ERF	APETALA2/ETHYLENE RESPONSE FACTOR
bHLH	Basic helix–loop–helix
BM	Branch meristem
BR	Brassinosteroid
CK	Cytokinin
FAC	Florigen activation complex
FM	Flower meristem
GA	Gibberellic acid
HD-Zip	Homeodomain leucine zipper
IM	Inflorescence meristem
LD	Long day
PS	Pedicellate spikelet
SAM	Shoot apical meristem
SD	Short day
SpM	Spikelet meristem
SS	Sessile spikelet
TCP	Teosinte branched/Cycloidea/PCF
TF	Transcription factor
SL	Strigolactone

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References

Abe M et al (2005) FD, a bZIP protein mediating signals from the floral pathway integrator FT at the shoot apex. Science 309:1052–1056. https://doi.org/10.1126/science.1115983

Acosta I et al (2009) Tasselseed1 is a lipoxygenase affecting jasmonic acid signaling in sex determination of maize. Science 323:262–265

Andres F, Coupland G (2012) The genetic basis of flowering responses to seasonal cues. Nat Rev Genet 13:627–639. https://doi.org/10.1038/nrg3291

Ashikari M et al (2005) Cytokinin oxidase regulates rice grain production. Science 309:741–745. https://doi.org/10.1126/science.1113373

Bai X et al (2017) Duplication of an upstream silencer of FZP increases grain yield in rice. Nat Plants 3:885–893. https://doi.org/10.1038/s41477-017-0042-4

Balasubramanian S, Sureshkumar S, Lempe J, Weigel D (2006) Potent induction of *Arabidopsis thaliana* flowering by elevated growth temperature. PLoS Genet 2:e106. https://doi.org/10.1371/journal.pgen.0020106

Bell EM et al (2012) Arabidopsis lateral organ boundaries negatively regulates brassinosteroid accumulation to limit growth in organ boundaries. Proc Natl Acad Sci USA

109:21146–21151. https://doi.org/10.1073/pnas.1210789109
Boden SA et al (2015) Ppd-1 is a key regulator of inflorescence architecture and paired spikelet development in wheat. Nat Plants 1:1–6. https://doi.org/10.1038/Nplants.2014.16
Bommert P, Satoh-Nagasawa N, Jackson D, Hirano HY (2005) Genetics and evolution of inflorescence and flower development in grasses. Plant Cell Physiol 46:69–78. https://doi.org/10.1093/pcp/pci504
Cai Q et al (2014) Jasmonic acid regulates spikelet development in rice. Nat Commun 5:3476. https://doi.org/10.1038/ncomms4476
Callens C, Tucker MR, Zhang D, Wilson ZA (2018) Dissecting the role of MADS-box genes in monocot floral development and diversity. J Exp Bot 69:2435–2459. https://doi.org/10.1093/jxb/ery086
Chandler JW (2018) Class VIIIb APETALA2 ethylene response factors in plant development. Trends Plant Sci 23:151–162. https://doi.org/10.1016/j.tplants.2017.09.016
Chen K, Wang Y, Zhang R, Zhang H, Gao C (2019) CRISPR/Cas genome editing and precision plant breeding in agriculture. Annu Rev Plant Biol 70:667–697. https://doi.org/10.1146/annurev-arplant-050718-100049
Chen L, Zhao J, Song J, Jameson PE (2020) Cytokinin dehydrogenase: a genetic target for yield improvement in wheat. Plant Biotechnol J 18:614–630. https://doi.org/10.1111/pbi.13305
Chuck G, Muszynski M, Kellogg E, Hake S, Schmidt RJ (2002) The control of spikelet meristem identity by the *branched silkless1* gene in maize. Science 298:1238–1241
Corbesier L et al (2007) FT protein movement contributes to long-distance signaling in floral induction of Arabidopsis. Science 316:1030–1033. https://doi.org/10.1126/science.1141752
Dai Z, Wang J, Yang X, Lu H, Miao X, Shi Z (2018) Modulation of plant architecture by the miR156f–OsSPL7–OsGH3.8 pathway in rice. J Exp Bot 69:5117–5130. https://doi.org/10.1093/jxb/ery273
Dampanaboina L et al (2019) Sorghum MSD3 encodes an ω-3 fatty acid desaturase that increases grain number by reducing jasmonic acid levels. Int J Mol Sci 20:5359
Danilevskaya ON, Meng X, Ananiev EV (2010) Concerted modification of flowering time and inflorescence architecture by ectopic expression of *TFL1*-like genes in maize. Plant Physiol 153:238–251. https://doi.org/10.1104/pp.110.154211
Deng W, Casao MC, Wang P, Sato K, Hayes PM, Finnegan EJ, Trevaskis B (2015) Direct links between the vernalization response and other key traits of cereal crops. Nat Commun 6:5882. https://doi.org/10.1038/ncomms6882
Derbyshire P, Byrne ME (2013) MORE SPIKELETS1 is required for spikelet fate in the inflorescence of Brachypodium. Plant Physiol 161:1291–1302. https://doi.org/10.1104/pp.112.212340
Dixon LE, Farre A, Finnegan EJ, Orford S, Griffiths S, Boden SA (2018a) Developmental responses of bread wheat to changes in ambient temperature following deletion of a locus that includes FLOWERING LOCUS T1. Plant Cell Environ 41:1715–1725. https://doi.org/10.1111/pce.13130
Dixon LE et al (2018b) *TEOSINTE BRANCHED1* regulates inflorescence architecture and development in bread wheat (*Triticum aestivum*). Plant Cell 30:563–581. https://doi.org/10.1105/tpc.17.00961
Doebley J, Stec A, Hubbard L (1997) The evolution of apical dominance in maize. Nature 386:485–488. https://doi.org/10.1038/386485a0
Doebley JF, Gaut BS, Smith BD (2006) The molecular genetics of crop domestication. Cell 127:1309–1321. https://doi.org/10.1016/j.cell.2006.12.006
Du A et al (2017) The DTH8-Hd1 module mediates day-length-dependent regulation of rice flowering. Mol Plant 10:948–961. https://doi.org/10.1016/j.molp.2017.05.006
Endress PK (2010) Disentangling confusions in inflorescence morphology: patterns and diversity of reproductive shoot ramification in angiosperms. J Syst Evol 48:225–239. https://doi.org/10.1111/j.1759-6831.2010.00087.x
Ferrandiz C, Gu Q, Martienssen R, Yanofsky MF (2000) Redundant regulation of meristem identity and plant architecture by FRUITFULL, APETALA1 and CAULIFLOWER. Development 127:725–734
Finnegan EJ et al (2018) Zebularine treatment is associated with deletion of FT-B1 leading to an increase in spikelet number in bread wheat. Plant Cell Environ 41:1346–1360. https://doi.org/10.1111/pce.13164
Gallavotti A et al (2004) The role of *barren stalk1* in the architecture of maize. Nature 432:630–635. https://doi.org/10.1038/nature03148
Gallavotti A, Barazesh S, Malcomber S, Hall D, Jackson D, Schmidt RJ, McSteen P (2008a) *Sparse inflorescence1* encodes a monocot-specific *YUCCA*-like gene required for vegetative and reproductive development in maize. Proc Natl Acad Sci USA 105:15196–15201. https://doi.org/10.1073/pnas.0805596105
Gallavotti A, Yang Y, Schmidt RJ, Jackson D (2008b) The Relationship between auxin transport and maize branching. Plant Physiol 147:1913–1923. https://doi.org/10.1104/pp.108.121541
Gao H et al (2014) Days to heading 7, a major quantitative locus determining photoperiod sensitivity and regional adaptation in rice. Proc Natl Acad Sci 111:16337–16342. https://doi.org/10.1073/pnas.1418204111
Gao XQ, Wang N, Wang XL, Zhang XS (2019) Architecture of wheat inflorescence: insights from rice. Trends Plant Sci 24:802–809. https://doi.org/10.1016/j.tplants.2019.06.002
Gauley A, Boden SA (2019) Genetic pathways controlling inflorescence architecture and development in wheat and barley. J Integr Plant Biol 61:296–309. https://doi.org/10.1111/jipb.12732
Gendron JM et al (2012) Brassinosteroids regulate organ boundary formation in the shoot apical meristem of Arabidopsis. Proc Natl Acad Sci USA 109:21152–21157. https://doi.org/10.1073/pnas.1210799110
Gladman N et al (2019) Fertility of pedicellate spikelets in sorghum is controlled by a jasmonic acid regulatory module. Int J Mol Sci 20:4951
Golan G et al (2019) GNI-A1 mediates trade-off between grain number and grain weight in tetraploid wheat. Theor Appl Genet 132:2353–2365. https://doi.org/10.1007/s00122-019-03358-5
Gou J et al (2017) The miR156-SPL4 module predominantly regulates aerial axillary bud formation and controls shoot architecture. New Phytol 216:829–840. https://doi.org/10.1111/nph.14758
Gou J et al (2019) SPL7 and SPL8 represent a novel flowering regulation mechanism in switchgrass. New Phytol 222:1610–1623. https://doi.org/10.1111/nph.15712
Grierson CS et al (2011) One hundred important questions facing plant science research. New Phytol 192:6–12. https://doi.org/10.1111/j.1469-8137.2011.03859.x
Halliwell J et al (2016) Systematic investigation of FLOWERING LOCUS T-like poaceae gene families identifies the short-day expressed flowering pathway gene, TaFT3 in wheat (*Triticum aestivum* L.). Front Plant Sci 7:857. https://doi.org/10.3389/fpls.2016.00857

Han Y, Zhang C, Yang H, Jiao Y (2014) Cytokinin pathway mediates APETALA1 function in the establishment of determinate floral meristems in Arabidopsis. Proc Natl Acad Sci USA 111:6840–6845. https://doi.org/10.1073/pnas.1318532111

Hanano S, Goto K (2011) Arabidopsis TERMINAL FLOWER1 is involved in the regulation of flowering time and inflorescence development through transcriptional repression. Plant Cell 23:3172–3184. https://doi.org/10.1105/tpc.111.088641

Hayama R, Yokoi S, Tamaki S, Yano M, Shimamoto K (2003) Adaptation of photoperiodic control pathways produces short-day flowering in rice. Nature 422:719–722. https://doi.org/10.1038/nature01549

Hemming MN, Peacock WJ, Dennis ES, Trevaskis B (2008) Low-temperature and daylength cues are integrated to regulate FLOWERING LOCUS T in barley. Plant Physiol 147:355–366. https://doi.org/10.1104/pp.108.116418

Hickey LT et al (2019) Breeding crops to feed 10 billion. Nat Biotechnol 37:744–754. https://doi.org/10.1038/s41587-019-0152-9

Ho WW, Weigel D (2014) Structural features determining flower-promoting activity of Arabidopsis FLOWERING LOCUS T. Plant Cell 26:552–564. https://doi.org/10.1105/tpc.113.115220

Houston K et al (2013) Variation in the interaction between alleles of HvAPETALA2 and microRNA172 determines the density of grains on the barley inflorescence. Proc Natl Acad Sci USA 110:16675–16680. https://doi.org/10.1073/pnas.1311681110

Hu Y et al (2015) Interactions of OsMADS1 with floral homeotic genes in rice flower development. Mol Plant 8:1366–1384. https://doi.org/10.1016/j.molp.2015.04.009

Huang P et al (2017) Sparse panicle1 is required for inflorescence development in *Setaria viridis* and maize. Nat Plants 3:17054. https://doi.org/10.1038/nplants.2017.54

Hwang I, Sheen J, Müller B (2012) Cytokinin signaling networks. Annu Rev Plant Biol 63:353–380. https://doi.org/10.1146/annurev-arplant-042811-105503

Imaizumi T, Tran HG, Swartz TE, Briggs WR, Kay SA (2003) FKF1 is essential for photoperiodic-specific light signalling in Arabidopsis. Nature 426:302–306. https://doi.org/10.1038/nature02090

Itoh H, Nonoue Y, Yano M, Izawa T (2010) A pair of floral regulators sets critical day length for Hd3a florigen expression in rice. Nat Genet 42:635–638. https://doi.org/10.1038/ng.606

Jiao Y et al (2010) Regulation of *OsSPL14* by OsmiR156 defines ideal plant architecture in rice. Nat Genet 42:541–544. https://doi.org/10.1038/ng.591

Jiao Y et al (2018) MSD1 regulates pedicellate spikelet fertility in sorghum through the jasmonic acid pathway. Nat Commun 9:822. https://doi.org/10.1038/s41467-018-03238-4

Kardailsky I et al (1999) Activation tagging of the floral inducer FT. Science 286:1962–1965

Kellogg EA (2001) Evolutionary history of the grasses. Plant Physiol 125:1198–1205

Kellogg EA, Camara PE, Rudall PJ, Ladd P, Malcomber ST, Whipple CJ, Doust AN (2013) Early inflorescence development in the grasses (Poaceae). Front Plant Sci 4:250. https://doi.org/10.3389/fpls.2013.00250

Kim JJ, Lee JH, Kim W, Jung HS, Huijser P, Ahn JH (2012) The microRNA156-SQUAMOSA PROMOTER BINDING PROTEIN-LIKE3 module regulates ambient temperature-responsive flowering via FLOWERING LOCUS T in Arabidopsis. Plant Physiol 159:461–478. https://doi.org/10.1104/pp.111.192369

Kobayashi Y, Kaya H, Goto K, Iwabuchi M, Araki T (1999) A pair of related genes with antagonistic roles in mediating flowering signals. Science 286:1960–1962. https://doi.org/10.1126/science.286.5446.1960

Kobayashi K et al (2012) Inflorescence meristem identity in rice is specified by overlapping functions of three AP1/FUL-like MADS box genes and *PAP2*, a SEPALLATA MADS box gene. Plant Cell 24:1848–1859. https://doi.org/10.1105/tpc.112.097105

Kojima S, Takahashi Y, Kobayashi Y, Monna L, Sasaki T, Araki T, Yano M (2002) Hd3a, a rice ortholog of the Arabidopsis FT gene, promotes transition to flowering downstream of Hd1 under short-day conditions. Plant Cell Physiol 43:1096–1105

Komatsu M, Chujo A, Nagato Y, Shimamoto K, Kyozuka J (2003) *FRIZZY PANICLE* is required to prevent the formation of axillary meristems and to establish floral meristem identity in rice spikelets. Development 130:3841–3850. https://doi.org/10.1242/dev.00564

Komatsuda T et al (2007) Six-rowed barley originated from a mutation in a homeodomain-leucine zipper I-class homeobox gene. Proc Natl Acad Sci 104:1424–1429. https://doi.org/10.1073/pnas.0608580104

Komiya R, Ikegami A, Tamaki S, Yokoi S, Shimamoto K (2008) *Hd3a* and *RFT1* are essential for flowering in rice. Development 135:767–774

Komiya R, Yokoi S, Shimamoto K (2009) A gene network for long-day flowering activates *RFT1* encoding a mobile flowering signal in rice. Development 136:3443–3450

Koppolu R, Schnurbusch T (2019) Developmental pathways for shaping spike inflorescence architecture in barley and wheat. J Integr Plant Biol 61:278–295. https://doi.org/10.1111/jipb.12771

Kurakawa T et al (2007) Direct control of shoot meristem activity by a cytokinin-activating enzyme. Nature 445:652–655

Kyozuka J (2014) Chapter seven—grass inflorescence: basic structure and diversity. In: Fornara F (ed) Advances in botanical research, vol 72. Academic Press, New York, pp 191–219. https://doi.org/10.1016/B978-0-12-417162-6.00007-9

Kyozuka J, Tokunaga H, Yoshida A (2014) Control of grass inflorescence form by the fine-tuning of meristem phase change. Curr Opin Plant Biol 17:110–115. https://doi.org/10.1016/j.pbi.2013.11.010

Leng Y et al (2020) Using Heading date 1 preponderant alleles from indica cultivars to breed high-yield, high-quality japonica rice varieties for cultivation in south China. Plant Biotechnol J 18:119–128. https://doi.org/10.1111/pbi.13177

Lewis MW, Bolduc N, Hake K, Htike Y, Hay A, Candela H, Hake S (2014) Gene regulatory interactions at lateral organ boundaries in maize. Development 141:4590–4597. https://doi.org/10.1242/dev.111955

Li Z, He Y (2020) Roles of brassinosteroids in plant reproduction. Int J Mol Sci 21:872

Li H et al (2009) A putative lipase gene *EXTRA GLUME1* regulates both empty-glume fate and spikelet development in rice. Plant J Cell Mol Biol 57:593–605. https://doi.org/10.1111/j.1365-313X.2008.03710.x

Li S et al (2013) Rice zinc finger protein DST enhances grain production through controlling *Gn1a*/*OsCKX2* expression. Proc Natl Acad Sci USA 110:3167–3172. https://doi.org/10.1073/pnas.1300359110

Li Y, Li X, Fu D, Wu C (2018) Panicle morphology mutant 1 (PMM1) determines the inflorescence architecture of rice by controlling brassinosteroid biosynthesis. BMC Plant Biol 18:348. https://doi.org/10.1186/s12870-018-1577-x

Li C, Lin H, Chen A, Lau M, Jernstedt J, Dubcovsky J (2019) Wheat *VRN1*, *FUL2* and *FUL3* play critical and redundant roles in spikelet development and spike determinacy. Development 146:dev175398. https://doi.org/10.1242/dev.175398

Liu Z, Mara C (2010) Regulatory mechanisms for floral homeotic gene expression. Semin Cell Dev Biol 21:80–86. https://doi.org/10.1016/j.semcdb.2009.11.012

Liu C et al (2013) A conserved genetic pathway determines inflorescence architecture in Arabidopsis and rice. Dev Cell 24:612–622. https://doi.org/10.1016/j.devcel.2013.02.013

Liu J, Cheng X, Liu P, Sun J (2017) miR156-targeted SBP-box transcription factors interact with DWARF53 to regulate TEOSINTE BRANCHED1 and BARREN STALK1 expression in bread wheat. Plant Physiol 174:1931–1948. https://doi.org/10.1104/pp.17.00445

Liu P, Liu J, Dong H, Sun J (2018) Functional regulation of Q by microRNA172 and transcriptional co-repressor TOPLESS in controlling bread wheat spikelet density. Plant Biotechnol J 16:495–506. https://doi.org/10.1111/pbi.12790

Liu H, Zhou X, Li Q, Wang L, Xing Y (2020) CCT domain-containing genes in cereal crops: flowering time and beyond. Theor Appl Genet. https://doi.org/10.1007/s00122-020-03554-8

Lyu J et al (2020) Neo-functionalization of a Teosinte branched 1 homologue mediates adaptations of upland rice. Nat Commun 11:725. https://doi.org/10.1038/s41467-019-14264-1

Miura K et al (2010) *OsSPL14* promotes panicle branching and higher grain productivity in rice. Nat Genet 42:545–549. https://doi.org/10.1038/ng.592

Mulki MA, Bi X, von Korff M (2018) FLOWERING LOCUS T3 controls spikelet initiation but not floral development. Plant Physiol 178:1170–1186. https://doi.org/10.1104/pp.18.00236

Nakagawa M, Shimamoto K, Kyozuka J (2002) Overexpression of *RCN1* and *RCN2*, rice *TERMINAL FLOWER 1/CENTRORADIALIS* homologs, confers delay of phase transition and altered panicle morphology in rice. Plant J Cell Mol Biol 29:743–750

Okada K, Ueda J, Komaki MK, Bell CJ, Shimura Y (1991) Requirement of the auxin polar transport system in early stages of Arabidopsis floral bud formation. Plant Cell 3:677–684. https://doi.org/10.1105/tpc.3.7.677

Pin PA, Benlloch R, Bonnet D, Wremerth-Weich E, Kraft T, Gielen JJ, Nilsson O (2010) An antagonistic pair of FT homologs mediates the control of flowering time in sugar beet. Science 330:1397–1400. https://doi.org/10.1126/science.1197004

Poursarebani N et al (2015) The genetic basis of composite spike form in barley and 'miracle-wheat'. Genetics 201:155–165. https://doi.org/10.1534/genetics.115.176628

Poursarebani N et al (2020) COMPOSITUM 1 (COM1) contributes to the architectural simplification of barley inflorescence via cell wall-mediated and meristem identity signals. bioRxiv. https://doi.org/10.1101/2020.02.18.952705

Putterill J, Varkonyi-Gasic E (2016) FT and florigen long-distance flowering control in plants. Curr Opin Plant Biol 33:77–82. https://doi.org/10.1016/j.pbi.2016.06.008

Putterill J, Robson F, Lee K, Simon R, Coupland G (1995) The *CONSTANS* gene of Arabidopsis promotes flowering and encodes a protein showing similarities to zinc finger transcription factors. Cell 80:847–857

Qian Q, Guo L, Smith SM, Li J (2016) Breeding high-yield superior quality hybrid super rice by rational design. Natl Sci Rev 3:283–294. https://doi.org/10.1093/nsr/nww006

Ramsay L et al (2011) INTERMEDIUM-C, a modifier of lateral spikelet fertility in barley, is an ortholog of the maize domestication gene TEOSINTE BRANCHED 1. Nat Genet 43:169–172. https://doi.org/10.1038/ng.745

Ren D et al (2013) MULTI-FLORET SPIKELET1, which encodes an AP2/ERF protein, determines spikelet meristem fate and sterile lemma identity in rice. Plant Physiol 162:872–884. https://doi.org/10.1104/pp.113.216044

Ren D et al (2018) 'Two-floret spikelet' as a novel resource has the potential to increase rice yield. Plant Biotechnol J 16:351–353. https://doi.org/10.1111/pbi.12849

Ren D et al (2019) FON4 prevents the multi-floret spikelet in rice. Plant Biotechnol J 17:1007–1009. https://doi.org/10.1111/pbi.13083

Ren D, Li Y, He G, Qian Q (2020) Multifloret spikelet improves rice yield. New Phytol 225:2301–2306. https://doi.org/10.1111/nph.16303

Rodriguez-Leal D, Lemmon ZH, Man J, Bartlett ME, Lippman ZB (2017) Engineering quantitative trait variation for crop improvement by genome editing. Cell 171(2):470–480.e8. https://doi.org/10.1016/j.cell.2017.08.030

Sakuma S, Schnurbusch T (2020) Of floral fortune: tinkering with the grain yield potential of cereal crops. New Phytol 225:1873–1882. https://doi.org/10.1111/nph.16189

Sakuma S et al (2013) Divergence of expression pattern contributed to neofunctionalization of duplicated HD-Zip I transcription factor in barley. New Phytol 197:939–948. https://doi.org/10.1111/nph.12068

Sakuma S et al (2019) Unleashing floret fertility in wheat through the mutation of a homeobox gene. Proc Natl Acad Sci 116:5182–5187. https://doi.org/10.1073/pnas.1815465116

Serrano-Mislata A, Bencivenga S, Bush M, Schiessl K, Boden S, Sablowski R (2017) DELLA genes restrict inflorescence meristem function independently of plant height. Nat Plants 3:749–754. https://doi.org/10.1038/s41477-017-0003-y

Song YH, Ito S, Imaizumi T (2013) Flowering time regulation: photoperiod- and temperature-sensing in leaves. Trends Plant Sci 18:575–583. https://doi.org/10.1016/j.tplants.2013.05.003

Song S, Wang G, Hu Y, Liu H, Bai X, Qin R, Xing Y (2018) OsMFT1 increases spikelets per panicle and delays heading date in rice by suppressing Ehd1, FZP and SEPALLATA-like genes. J Exp Bot 69:4283–4293. https://doi.org/10.1093/jxb/ery232

Soyk S et al (2017) Bypassing negative epistasis on yield in tomato imposed by a domestication gene. Cell 169:1142–1155.e1112. https://doi.org/10.1016/j.cell.2017.04.032

Tabuchi H et al (2011) *LAX PANICLE2* of rice encodes a novel nuclear protein and regulates the formation of axillary meristems. Plant Cell 23:3276–3287. https://doi.org/10.1105/tpc.111.088765

Tamaki S, Matsuo S, Wong HL, Yokoi S, Shimamoto K (2007) Hd3a protein is a mobile flowering signal in rice. Science 316:1033–1036. https://doi.org/10.1126/science.1141753

Tamaki S et al (2015) FT-like proteins induce transposon silencing in the shoot apex during floral induction in rice. Proc Natl Acad Sci USA 112:E901–910. https://doi.org/10.1073/pnas.1417623112

Taoka K-i et al (2011) 14-3-3 proteins act as intracellular receptors for rice Hd3a florigen. Nature 476:332–335

Turck F, Fornara F, Coupland G (2008) Regulation and identity of florigen: FLOWERING LOCUS T moves center stage. Annu Rev Plant Biol 59:573–594. https://doi.org/10.1146/annurev.arplant.59.032607.092755

Wang H, Wang H (2015) The miR156/SPL module, a regulatory hub and versatile toolbox, gears up crops for enhanced agronomic traits. Mol Plant 8:677–688. https://doi.org/10.1016/j.molp.2015.01.008

Wang JW, Czech B, Weigel D (2009) miR156-regulated SPL transcription factors define an endogenous flowering pathway in *Arabidopsis thaliana*. Cell 138:738–749. https://doi.org/10.1016/j.cell.2009.06.014

Wang S et al (2017) Non-canonical regulation of SPL transcription factors by a human OTUB1-like deubiquitinase defines a new plant type rice associated with higher grain yield. Cell Res 27:1142–1156. https://doi.org/10.1038/cr.2017.98

Wang B, Smith SM, Li J (2018) Genetic regulation of shoot architecture. Annu Rev Plant Biol 69:437–468. https://doi.org/10.1146/annurev-arplant-042817-040422

Wei X et al (2010) *DTH8* suppresses flowering in rice, influencing plant height and yield potential simultaneously. Plant Physiol 153:1747–1758. https://doi.org/10.1104/pp.110.156943

Wigge PA, Kim MC, Jaeger KE, Busch W, Schmid M, Lohmann JU, Weigel D (2005) Integration of spatial and temporal information during floral induction in Arabidopsis. Science 309:1056–1059. https://doi.org/10.1126/science.1114358

Wils CR, Kaufmann K (2017) Gene-regulatory networks controlling inflorescence and flower development in *Arabidopsis thaliana*. Biochim Biophys Acta Gene Regul Mech 1860:95–105. https://doi.org/10.1016/j.bbagrm.2016.07.014

Worthen JM, Yamburenko MV, Lim J, Nimchuk ZL, Kieber JJ, Schaller GE (2019) Type-B response regulators of rice play key roles in growth, development and cytokinin signaling. Development 146:dev174870. https://doi.org/10.1242/dev.174870

Wu G, Park MY, Conway SR, Wang JW, Weigel D, Poethig RS (2009) The sequential action of miR156 and miR172 regulates developmental timing in Arabidopsis. Cell 138:750–759. https://doi.org/10.1016/j.cell.2009.06.031

Wu MF, Yamaguchi N, Xiao J, Bargmann B, Estelle M, Sang Y, Wagner D (2015) Auxin-regulated chromatin switch directs acquisition of flower primordium founder fate. eLife 4:e09269. https://doi.org/10.7554/eLife.09269

Wu Y, Fu Y, Zhao S, Gu P, Zhu Z, Sun C, Tan L (2016) CLUSTERED PRIMARY BRANCH 1, a new allele of DWARF11, controls panicle architecture and seed size in rice. Plant Biotechnol J 14:377–386. https://doi.org/10.1111/pbi.12391

Wu F, Shi X, Lin X, Liu Y, Chong K, Theissen G, Meng Z (2017) The ABCs of flower development: mutational analysis of AP1/FUL-like genes in rice provides evidence for a homeotic (A)-function in grasses. Plant J Cell Mol Biol 89:310–324. https://doi.org/10.1111/tpj.13386

Wu D et al (2018) Loss of LOFSEP transcription factor function converts spikelet to leaf-like structures in rice. Plant Physiol 176:1646–1664. https://doi.org/10.1104/pp.17.00704

Xu H, Liu Q, Yao T, Fu X (2014) Shedding light on integrative GA signaling. Curr Opin Plant Biol 21:89–95. https://doi.org/10.1016/j.pbi.2014.06.010

Xue W et al (2008) Natural variation in *Ghd7* is an important regulator of heading date and yield potential in rice. Nat Genet 40:761–767. https://doi.org/10.1038/ng.143

Yamaguchi A, Wu MF, Yang L, Wu G, Poethig RS, Wagner D (2009) The microRNA-regulated SBP-Box transcription factor SPL3 is a direct upstream activator of LEAFY, FRUITFULL, and APETALA1. Dev Cell 17:268–278. https://doi.org/10.1016/j.devcel.2009.06.007

Yamaguchi N et al (2013) A molecular framework for auxin-mediated initiation of flower primordia. Dev Cell 24:271–282. https://doi.org/10.1016/j.devcel.2012.12.017

Yamaguchi N, Winter CM, Wu MF, Kanno Y, Yamaguchi A, Seo M, Wagner D (2014) Gibberellin acts positively then negatively to control onset of flower formation in Arabidopsis. Science 344:638–641. https://doi.org/10.1126/science.1250498

Yamburenko MV, Kieber JJ, Schaller GE (2017) Dynamic patterns of expression for genes regulating cytokinin metabolism and signaling during rice inflorescence development. PLoS ONE 12:e0176060. https://doi.org/10.1371/journal.pone.0176060

Yan L et al (2006) The wheat and barley vernalization gene VRN3 is an orthologue of FT. Proc Natl Acad Sci USA 103:19581–19586. https://doi.org/10.1073/pnas.0607142103

Yan WH et al (2011) A major QTL, *Ghd8*, plays pleiotropic roles in regulating grain productivity, plant height, and heading date in rice. Mol Plant 4:319–330. https://doi.org/10.1093/mp/ssq070

Yan W et al (2013) Natural variation in Ghd7.1 plays an important role in grain yield and adaptation in rice. Cell Res 23:969–971. https://doi.org/10.1038/cr.2013.43

Yang F, Wang Q, Schmitz G, Müller D, Theres K (2012) The bHLH protein ROX acts in concert with RAX1 and LAS to modulate axillary meristem formation in Arabidopsis. Plant J 71:61–70. https://doi.org/10.1111/j.1365-313X.2012.04970.x

Yang J et al (2017) Dynamic regulation of auxin response during rice development revealed by newly established hormone biosensor markers. Front Plant Sci 8:256. https://doi.org/10.3389/fpls.2017.00256

Yang J, Thames S, Best NB, Jiang H, Huang P, Dilkes BP, Eveland AL (2018) Brassinosteroids modulate meristem fate and differentiation of unique inflorescence morphology in *Setaria viridis*. Plant Cell 30:48–66. https://doi.org/10.1105/tpc.17.00816

Yao H et al (2019) The barren stalk2 gene is required for axillary meristem development in maize. Mol Plant 12:374–389. https://doi.org/10.1016/j.molp.2018.12.024

Yoo SY, Kardailsky I, Lee JS, Weigel D, Ahn JH (2004) Acceleration of flowering by overexpression of MFT (MOTHER OF FT AND TFL1). Mol Cells 17:95–101

Yoshida A, Suzaki T, Tanaka W, Hirano HY (2009) The homeotic gene *long sterile lemma* (*G1*) specifies sterile lemma identity in the rice spikelet. Proc Natl Acad Sci USA 106:20103–20108. https://doi.org/10.1073/pnas.0907896106

You X et al (2019) OsPEX5 regulates rice spikelet development through modulating jasmonic acid biosynthesis. New Phytol 224:712–724. https://doi.org/10.1111/nph.16037

Youssef HM et al (2017) VRS2 regulates hormone-mediated inflorescence patterning in barley. Nat Genet 49:157–161. https://doi.org/10.1038/ng.3717

Yu S et al (2012) Gibberellin regulates the *Arabidopsis* floral transition through miR156-targeted SQUAMOSA PROMOTER BINDING–LIKE transcription factors. Plant Cell 24:3320–3332. https://doi.org/10.1105/tpc.112.101014

Yu S, Lian H, Wang J-W (2015) Plant developmental transitions: the role of microRNAs and sugars. Curr Opin Plant Biol 27:1–7. https://doi.org/10.1016/j.pbi.2015.05.009

Yuan Z et al (2009) *RETARDED PALEA1* controls palea development and floral zygomorphy in rice. Plant Physiol 149:235–244. https://doi.org/10.1104/pp.108.128231

Yuan H et al (2017) 08SG2/OsBAK1 regulates grain size and number, and functions differently in Indica and Japonica backgrounds in rice. Rice 10:25. https://doi.org/10.1186/s12284-017-0165-2

Zhang D, Yuan Z (2014) Molecular control of grass inflorescence development. Annu Rev Plant Biol 65:553–578. https://doi.org/10.1146/annurev-arplant-050213-040104

Zhang Z et al (2011) Duplication and partitioning in evolution and function of homoeologous Q loci governing domestication characters in polyploid wheat. Proc Natl Acad Sci USA

108:18737–18742. https://doi.org/10.1073/pnas.1110552108
Zhang F, May A, Irish VF (2017a) Type-B ARABIDOPSIS RESPONSE REGULATORs directly activate WUSCHEL. Trends Plant Sci 22:815–817. https://doi.org/10.1016/j.tplants.2017.08.007
Zhang L et al (2017b) A natural tandem array alleviates epigenetic repression of IPA1 and leads to superior yielding rice. Nat Commun 8:14789. https://doi.org/10.1038/ncomms14789
Zhang T et al (2017c) LATERAL FLORET 1 induced the three-florets spikelet in rice. Proc Natl Acad Sci USA 114:9984–9989. https://doi.org/10.1073/pnas.1700504114
Zhang TQ, Lian H, Zhou CM, Xu L, Jiao Y, Wang JW (2017d) A two-step model for de novo activation of WUSCHEL during plant shoot regeneration. Plant Cell 29:1073–1087. https://doi.org/10.1105/tpc.16.00863
Zhao Y (2018) Essential roles of local auxin biosynthesis in plant development and in adaptation to environmental changes. Annu Rev Plant Biol 69:417–435. https://doi.org/10.1146/annurev-arplant-042817-040226
Zhao J et al (2015) Genetic interactions between diverged alleles of early heading date 1 (Ehd1) and heading date 3a (Hd3a)/RICE FLOWERING LOCUS T1 (RFT1) control differential heading and contribute to regional adaptation in rice (*Oryza sativa*). New Phytol 208:936–948. https://doi.org/10.1111/nph.13503
Zhou Y et al (2017) GNS4, a novel allele of DWARF11, regulates grain number and grain size in a high-yield rice variety. Rice 10:34. https://doi.org/10.1186/s12284-017-0171-4
Zhu Y, Wagner D (2020) Plant inflorescence architecture: the formation, activity, and fate of axillary meristems. Cold Spring Harbor Perspect Biol 12:a034652. https://doi.org/10.1101/cshperspect.a034652
Zhu S et al (2017) The OsHAPL1–DTH8–Hd1 complex functions as the transcription regulator to repress heading date in rice. J Exp Bot 68:553–568. https://doi.org/10.1093/jxb/erw468
Zwirek M, Waugh R, McKim SM (2019) Interaction between row-type genes in barley controls meristem determinacy and reveals novel routes to improved grain. New Phytol 221:1950–1965. https://doi.org/10.1111/nph.15548