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REVIEW ARTICLE

The Impact of Fasciation on Maize Inflorescence Architecture

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Abstract
How functional genetics research can be applied to improving crop yields is a timely challenge. One of the most direct methods is to produce larger inflorescences with higher productivity, which should be accompanied by a balance between stem cell proliferation and lateral organ initiation in meristems. Unbalanced proliferation of stem cells causes the fasciated inflorescences, which reflect the abnormal proliferation of meristems, derived from the Latin word 'fascis', meaning 'bundle'. Maize, a model system for grain crops, has shown tremendous yield improvements through the mysterious transformation of the female inflorescence during domestication. In this review, we focus on maize inflorescence architecture and highlight the patterns of fasciation, including recent progress.

Keywords Maize · Inflorescence architecture · Fasciation · Crop yields

Introduction

Maize is one of the most widely cultivated crops in the world, and one of the most important cereal crops along with wheat and rice. Based on the statistics of the Food and Agriculture Organization (FAO), the total production of maize, 1 billion tons, surpasses that of wheat and rice (Yang et al. 2017). This highest productivity of maize among cereal crops has been achieved through prolonged historical human efforts, called domestication, and advances in modern agricultural technology. Maize was domesticated starting ~ 10,000 years ago in Mexico (Harlan 1992; Wang et al. 1999), and has shown remarkable changes in plant architecture from its ancestor, teosinte (*Zea mays* ssp. *Parviglumis*) (Doebley 2004; Benz 2001; Doebley and Stec 1993). Teosinte produces many branches and tillers; however, domesticated modern maize generally produces few tillers or branches, and large ears, the female inflorescences. The transformation of the ear is especially mysterious, compared to other crops (Doebley 2004). How could this incredible domestication occur in maize? The first possibility is that the maize genome has a variety of active transposons (Mc 1950; Schnable et al. 2009) that promote spontaneous and frequent mutations, leading to transformations. The second possibility is that maize is a typical monoecious plant, indicating that it cross-pollinates. During domestication, many useful traits may have appeared and accumulated (Fu et al. 2002; Brunner et al. 2005). The natural cross-pollination could facilitate easier domestication from teosinte (Yang et al. 2017; van Heerwaarden et al. 2011; Piperno et al. 2009). As a result, two rows of kernels on teosinte ears have been domesticated to produce eight to 20 rows on the ears in maize (Doebley 2004). This remarkable increase in

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the number of kernels per ear is an outstanding feature of domesticated maize.

Many maize mutants defective in shoot apical meristem (SAM) have been selected to investigate and enhance this feature. Interestingly, mutants with dramatically enlarged inflorescence meristems (IMs) showed only a slight increase in the size of vegetative SAMs (Taguchi-Shiobara et al. 2001; Bommert et al. 2013a; Je et al. 2016, 2018), suggesting that the maize genome evolved to promote development of IMs rather than vegetative SAMs during domestication. This intense selection for larger inflorescences has made maize one of the best model crops for studying functional genetics in IM development and offers a great opportunity to identify useful genes for application in yield improvement. A number of mutants with defects in IM, such as those with fasciated ears, have been studied in maize. However, strong fasciated ear mutants do not improve productivity, due to a stunted ear, even though they increase kernel row number (KRN) (Bommert et al. 2013b; Je et al. 2016). To overcome this, maize targeting-induced local lesions in genomes (TILLING) lines with targeted EMS (ethyl methane sulfonate) mutagenesis (Bommert et al. 2013b; Till et al. 2004; Je et al. 2016) were used to isolate weak alleles with moderate IM phenotypes. Compared with strong fasciation mutants, mildly fasciated ear mutants show more potential to improve yield (Bommert et al. 2013b; Je et al. 2016). The TILLING or targeted EMS mutagenesis requires a lot of time and effort. Recent CRISPR/Cas gene-editing techniques make the identification of weak alleles much easier and faster (Shelake et al. 2019; Jinek et al. 2012; Liu et al. 2021b). As the CRISPR/Cas system continues to evolve, it could enable more delicate control over the IM by targeting single bases for editing (Komor et al. 2016; Gaudelli et al. 2017; Shelake et al. 2019; Liu et al. 2021b).

A deep understanding of the genetics underlying development of IMs is crucial for the synergistic application of recent genomic and technological advances in improving crop yields. In this review, we will discuss the maize inflorescence architecture and highlight the various patterns of fasciation to answer this question.

Sex Determination in Maize Inflorescences

Maize separates male and female flowers into different inflorescences on the same plant (Figs. 1, 2), termed monoecious. In the vegetative stage, maize SAMs continuously initiate lateral organs including leaves and axillary buds. After the transition to flowering, the SAM terminates with the production of the male inflorescence, or tassel (Bennetzen and Hake 2009). Interestingly, if the main stalk of maize is broken or removed during the seedling stage, a tiller will replace the broken main stalk. However, the tiller often grows without developing axillary ears, and terminates with the production of a feminized inflorescence, instead of a tassel. The tassel produces several branch meristems (BMs) (Fig. 1A) (Tanaka et al. 2013), whereas axillary buds gives rise to ears, which lack BMs (Fig. 1B). However, three classical mutants,

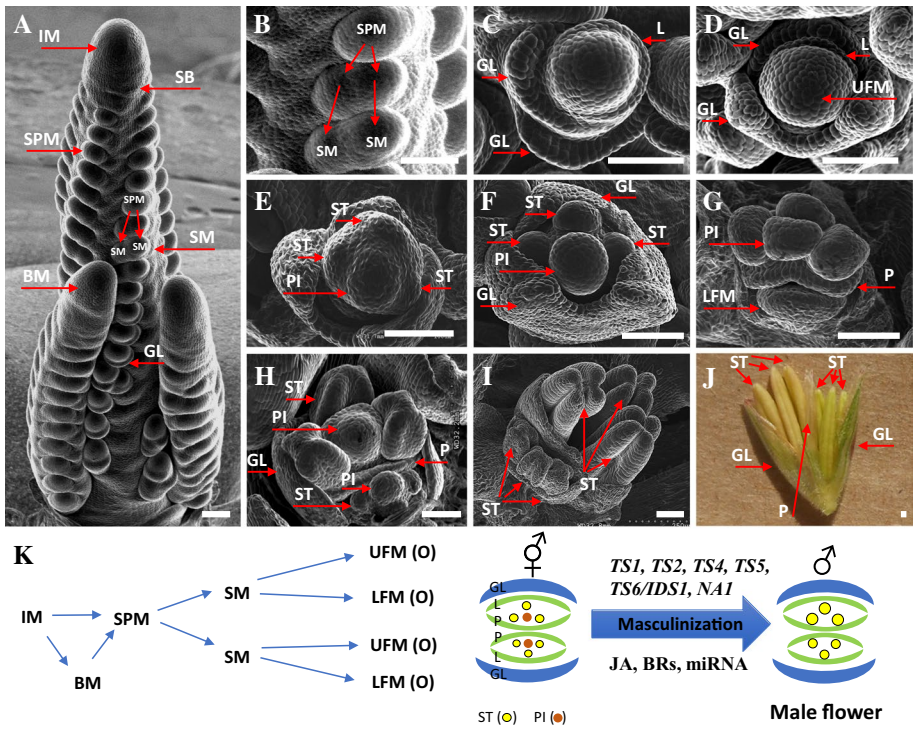

Fig. 1 Masculinization of the tassel, the male inflorescence in maize. **A–I** Scanning electron microscopy images (SEMs) of maize tassel development. **A** Immature tassel produces BMs and regular phyllotaxy of SPMs in the axils of suppressed bracts (SB). **B** SPMs divide into two SMs. **C, D** SMs form two glume (GL) primordia and give rise to two FMs, the upper (UFM) and lower (LFM). **E, F** The UFM forms floral organ primordia. **G–I** Removal of the GL reveals the LFM that forms floral organ primordia. **J** A mature male spikelet has two florets. **K** Schematic representation of reproductive meristem transition in tassel (left) and masculinization of spikelet (right). L, lemma; P, palea; ST, stamen; PI, pistil. Scale bars: 100 µm

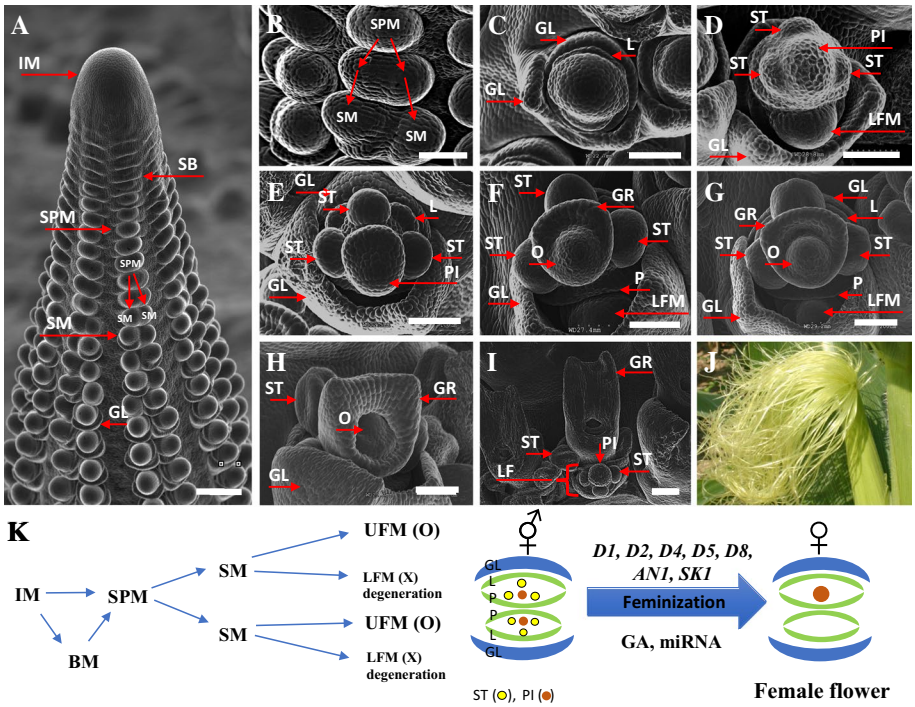

Fig. 2 Feminization of ear, the female inflorescence in maize. **A–I** SEMs of maize ear development. **A** Immature ear shows regular phyllotaxy of SPMs in the axils of suppressed bracts (SB). **B** SPMs divide into two SMs. **C, D** SMs form two glume (GL) primordia and gives rise to two FMs, the upper (UFM) and lower (LFM). **E–H** The UFM forms floral organ primordia and the peripheral cells of the carpel form a gynoecial ridge (GR), which becomes a long stigma called the silk. **I** Removal of the GL reveals the LFM, which also forms floral organ primordia but aborts early in development. **J** A clump of silks grows from the tip of the ear. **K** Schematic representation of reproductive meristem transition in ear (left) and feminization of spikelet (right). L, lemma; P, palea; ST, stamen; PI, pistil; O, ovule. Scale bars: 100 µm

ramosa1 (*ra1*), *ra2* and *ra3* encoding a zinc-finger transcription factor, a LOB domain transcription factor, and a trehalose-6-phosphate phosphatase, respectively, produce many branches in ears (Vollbrecht et al. 2005; Bortiri et al. 2006; Satoh-Nagasawa et al. 2006), suggesting that branching in ears is under transcriptional control and sugar signaling. Maize inflorescences progress through several stages to produce the final florets (Fig. 1). After production of BMs, the male IM and BMs produces spikelet pair meristems (SPMs) in a uniform phyllotaxy (Fig. 1A). SPMs give rise to a pair of spikelet meristems (SMs) (Fig. 1B). SMs subsequently divide into two floral meristems (FMs), upper (UFM) and lower FM (LFM) (Fig. 1G–I). As the final outcome, each SPM in the tassel produces four florets (Fig. 1K) (Gallavotti et al. 2008). In the beginning, the tassel FMs develop all floral organ primordia, such as perianth organs, pistils, and stamens (Fig. 1E–H), but the female pistil degenerates during maturation (Fig. 1I). This degeneration is under control of the male sex determinants, masculinizing genes (Fig. 1K), such as *tasselseed* (*ts*) named after the mutant phenotype (Dellaporta and Calderon-Urrea 1994). *TS1* and *TS2* encode a *LIPOXYGENASE* and an *ALCOHOL DEHYDROGENASE* respectively. These mutants are rescued by exogenous jasmonic acid (JA) application, suggesting that JA is involved in masculinization functions of *TS1* and *TS2* (DeLong et al. 1993; Acosta et al. 2009). The dominant *Ts5* mutant overexpresses *Zea mays* (*Zm*) *CYP94B1*, and develops a tasselseed phenotype through affecting JA catabolism (Wang et al. 2020; Lunde et al. 2019). In contrast, *TS4* encodes a microRNA that controls sex determination by targeting *TS6/indeterminate spikelet1* (*IDS1*), which encodes an *APETALA2*-like transcription factor (Chuck et al. 1998, 2007b). The maize brassinosteroid (BR) biosynthetic mutant, *nana plant1* (*na1*) encodes a *DET2* homolog, and also has a tasselseed phenotype (Hartwig et al. 2011). Taken together, male sex determinants are involved in the actions of miRNAs and BR and JA hormones (Fig. 1K).

Like the tassel IM, the ear IM initiates SPMs (Fig. 2A), which give rise to a pair of SMs and the SMs subsequently produce two FMs (Fig. 2B). The two FMs initiate floral organ primordia (Fig. 2D–I). However, only the pistil of the upper (primary) floret matures, and all floral organs in the lower (secondary) floret abort (Fig. 2I–K). As a final outcome, each SPM in the ear produces two fertile florets (Fig. 2K). During floral development, the upper peripheral cells of the carpel primordia are recruited to form the

gynoecial ridge that extends into a very long stigma, the pollen-attracting silk (Fig. 2F–J). Degeneration of male organs in the ear is under control of female sex determinants, or feminizing genes (Fig. 2K). These genes were identified as *dwarf* (*d*) mutants, *d1*, *d2*, *d3*, *d5*, *D8*, and *anther ear1* (*an1*), which develop perfect flowers without stamen abortion in the upper ear florets (Dellaporta and Calderon-Urrea 1994). These mutations encode genes involved in gibberellin (GA) biosynthesis or signaling (Andersen et al. 2005; Dellaporta and Calderon-Urrea 1994; Bensen et al. 1995). *SILKLESS1* (*SK1*), which encodes a miRNA targeting *TS2*, acts as a pistil protector (Malcomber and Kellogg 2006; Parkinson et al. 2007). These findings suggest that female sex determinants function in actions of miRNA and GA.

Maize Domestication, Focusing on Inflorescence Architecture

Domestication of crops involves numerous changes in plant morphology and is achieved through selection of mutations and accumulation of beneficial traits. The monoecy of maize could facilitate the accumulation of many agricultural traits by easy natural outcrossing (Dellaporta and Calderon-Urrea 1994). The various active transposons in the maize genome also promote spontaneous mutations that affect gene expression or function (Mc 1950; Schnable et al. 2009). In fact, ~ 85% of the maize genome is made up of transposon elements (TEs) (Schnable et al. 2009). For example, one of the most important traits of domestication arose through the activity of a TE. A *hopscotch* retrotransposon inserted approximately 58 kb upstream of the *teosinte branched1* (*tb1*) gene (Studer et al. 2011; Clark et al. 2006), results in overexpression of this gene in domesticated maize. *TB1* encodes a TB1-CYCLOIDEA-PROLIFERATING CELL FACTOR (TCP) transcription factor that acts as a repressor of axillary bud growth and enables the formation of female inflorescences (Doebley et al. 1997). *TB* also controls many other domestication genes (Dong et al. 2019), for example, it positively regulates *GRASSY TILLERS1* (*GT1*), which encodes a homeodomain-leucine zipper (HD-ZIP) transcription factor that represses tillering and ear prolificacy (Wills et al. 2013; Whipple et al. 2011). These domestication traits increase the apical dominance and concentrate the resources in the main stem of the plant, contributing to increase in size of the inflorescences (Doebley et al. 1997; Wills et al. 2013). TB1 also directly targets *teosinte glume architecture1* (*tga1*) and *tassels replace upper ears1* (*tru1*) by binding to the promoters of these genes (Studer et al. 2017; Dong et al. 2017). Single amino acid change in *tga1*, which encodes a SQUAMOSA PROMOTER BINDING PROTEIN (SBP) transcription factor, exposes the kernel by softening and reduction of the glumes (Wang et al. 2005, 2015). *tru1* encodes a BTB/POZ ankyrin repeat protein, and the mutants are highly branched with long axillary branches tipped by tassels instead of ears (Dong et al. 2017, 2019), suggesting that *TRU1* also functions as a sex determinant downstream of *TB1*. These effects of *tb1* on phenotype vary with genetic background (Doebley et al. 1995). *enhancer of tb1.2* (*etb1.2*) maps to a YABBY transcription factor *ZmYAB2.1*, also called *Zmshattering1-1* (*Zmsh1-1*), which is expressed in a narrow band of cells subtending the spikelet pair, the future abscission zone (Yang et al. 2016; Lin et al. 2012). *tb1* acts as a repressor of *ZmYAB2.1*, reducing seed shattering, also called known as non-disarticulation (Stitzer and Ross-Ibarra 2018). The MADS-box transcription factor *Zea agamous-like1* (*zagl1*) is also involved in seed shattering (Weber et al. 2008), suggesting that this trait is associated with various loci. Although domestication traits related to axillary branching/tiller and growth of glumes have been identified, some IM architecture traits, such as maturation of paired spikelets and inflorescence shift in phyllotaxy from alternating pattern in teosinte with a two-ranked ear to whorled pattern in maize with more than four ranked ear, remain unclear (Stitzer and Ross-Ibarra 2018). Teosinte develops only single mature spikelets, whereas maize has paired spikelets, and this variation is associated with variants on chromosomes 1 and 3 (Doebley and Stec 1991, 1993). *Zea floricaula/leafy2* (*zfl2*) is a candidate locus for inflorescence phyllotaxy differences between maize and teosinte, and shows associations with the ear rank trait in maize-teosinte hybrid populations. An additional QTL, *zfl1*, may alter the effect of *zfl2* (Bomblies and Doebley 2006; Briggs et al. 2007), however, *zfl1;zfl2* double mutants have a normal whorled pattern of axillary meristems initiation (Bomblies and Doebley 2006; Bomblies et al. 2003), suggesting that *zfl2* itself was not selected, but a linked gene acting through *zfl2* was selected during domestication (Bomblies and Doebley 2006). Although the genetic basis of the shift in inflorescence phyllotaxy from alternating to a whorled pattern remains unclear, many enlarged IM mutants are associated with an increase in ear rank (Taguchi-Shiobara et al. 2001; Bommert et al. 2013b, 2005; Je et al. 2016).

Maize Produces Inflorescences with Dome-Shaped Apical Meristems

Vegetative SAMs in maize form axillary organs in an alternate pattern, whereas after transition to flowering, IMs form multiple axillary organs in a whorled pattern (Giulini et al. 2004; Jackson and Hake 1999; Yang et al. 2015; Gallavotti et al. 2008). During the vegetative to reproductive transition, the diameter of the dome-shaped SAM increases approximately 1.5- to 2-fold in the B73 inbred line (Fig. 3A–C) (Bommert et al. 2013a, 2013b; Je et al. 2016; Leiboff et al.

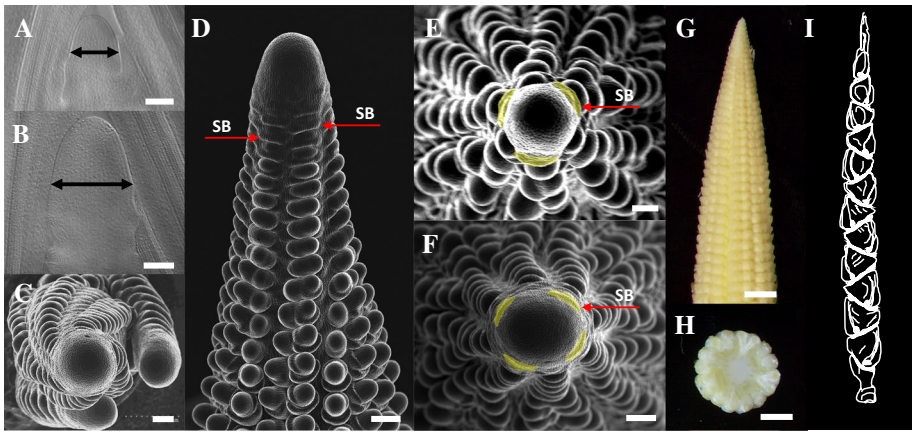

Fig. 3 Wild-type inflorescences with dome-shaped apices. **A, B** Cleared images of vegetative SAM and tassel IM from wild type. **C–F** SEMs of IMs from wild type. **C, D** Top view of a tassel IM and side view of ear IM shows the dome-shaped apex. **E, F** Top views of ear IMs show the whorled pattern of axillary organ initiation. The suppressed bracts are shaded in yellow, and alternate with adjacent ones. Red arrows indicate suppressed bracts (SBs). **G, H** Side and cross-section images of immature ears show single-tipped apex and whorled pattern of spikelets. **I** Diagrammatic illustration of a teosinte ear shows an alternate pattern of kernel rows. Scale bars: 100 μm in **A**–**F**; 1 cm in **G, H**

2016, 2015). However, this increased size does not affect the general morphology of the IM, which remains as a dome-shaped apex (Fig. 3C–F). Increase in SAM diameter results in a squared increase in surface area, and a cubic increase in volume, suggesting that the IM has sufficient stem cells and space for the increased number of axillary organ rows compared to vegetative SAM. The whorled pattern of axillary organs in the IM can be thought of as an increased number of axes in an alternate pattern, as each axillary organ alternates with its neighboring ones (Fig. 3E, F).

Depending on nutritional status or genetic background, the dome-shaped apex of the IM enlarges slightly to produce more axillary organ rows (Fig. 3E–H) (Bommert et al. 2013b). The meristem size in teosinte is smaller compared to domesticated maize varieties (Leiboff et al. 2016) and continues to initiate axillary organs in an alternate pattern even after conversion to the IM (Fig. 3I).

The Regulation of IM Size in Maize

Regulation by Signaling Transduction

The size of the IM is determined by the proliferative activity of the SAM (Kitagawa and Jackson 2019; Liu et al. 2021b). The SAM resides at the shoot apex and consists of specialized microdomains, the organizing center (OC), stem cell niches of central zone (CZ), peripheral zone (PZ), differentiation zone, and rib zone (RZ) (Heidstra and Sabatini 2014; Morrison and Spradling 2008). The OC is surrounded by and communicates closely with other domains to maintain SAM homeostasis (Wu et al. 2018b). The well-known communication system in the SAM is the CLAVATA-WUSCHEL (CLV-WUS) negative feedback circuit (Brand et al. 2000; Schoof et al. 2000; Stahl and Simon 2010). CLV signaling pathway is initiated in the CZ by secretion of the CLV3 peptide signal, which is recognized by leucine-rich repeat receptor-like kinase (LRR-RLK) CLV1 (Clark et al. 1997; Fletcher et al. 1999; Jeong et al. 1999). CLV signaling restricts *WUS* expression to the OC (Brand et al. 2000; Schoof et al. 2000). In turn, the homeodomain transcription factor WUS activates stem cell fate non-cell-autonomously to directly promote *CLV3* expression (Daum et al. 2014; Yadav et al. 2011). This CLV-WUS negative feedback signaling was first identified in *Arabidopsis*, but is also widely conserved in grasses (Somssich et al. 2016). In maize, *THICK TASSEL DWARF1* (*TD1*) and *FASCIATED EAR2* (*FEA2*) encode receptor-like proteins orthologous to *CLV1* and *CLV2*, respectively, and regulate the size of the tassel and ear IM (Bommert et al. 2005; Taguchi-Shiobara et al. 2001). *FEA2* is broadly expressed in the SAM, similar to *CLV2* in *Arabidopsis* (Jeong et al. 1999; Taguchi-Shiobara et al. 2001), suggesting that the function of *CLV2/FEA2* is conserved in maize. However, unlike *CLV1* (Clark et al. 1997), *TD1* is expressed in the PZ of vegetative SAMs and in the outermost layers of the IMs (Bommert et al. 2005), suggesting that *TD1* functions have diversified in maize. Two *WUS* orthologs in maize, *ZmWUS1* and *ZmWUS2* were identified by phylogenetic analysis (Nardmann and Werr 2006). *ZmWUS1* expression is very weak in the vegetative SAM (Nardmann and Werr 2006), but is detected clearly in the OC of the late vegetative SAM (Je et al. 2016), suggesting that the function of *ZmWUS1* is conserved in maize. Maize *CLV3/EMBRYO-SURROUNDING REGION7* (*ZmCLE7*), a

CLV3 ortholog identified by phylogenetic analysis in maize, is expressed in the L1 layer in IMs and in the CZ of SMs (Chen et al. 2021), and functions as a negative regulator of the meristem (Je et al. 2016). A CRISPR-Cas9 mutant (*Zmcle7*^{CR}) and weak promoter alleles *Zmcle7*$^{CR\text{-}pro}$ have enlarged IMs (Rodriguez-Leal et al. 2019; Liu et al. 2021a). ZmCLE7 peptide treatment inhibits SAM growth (Je et al. 2016), and triarabinosylated ZmCLE7 peptide is more potent (Je et al. 2018; Lee et al. 2020). *ZmCLE1E5* is a related CLE gene that is upregulated in *Zmcle7* mutants, and also expressed in the tips of IMs and in the CZ of SMs (Liu et al. 2021a). *Zmcle1e5* mutants enlarge the size of IMs but do not form fasciated ears, though they enhance the fasciation of *Zmcle7* (Liu et al. 2021a). The signaling pathways between CLV and WUS are not clear in maize, but downstream interacting components of FEA2/CLV2 have been identified. *COMPACT PLANT2* (*CT2*), encoding a heterotrimeric G protein alpha subunit (Bommert et al. 2013a) overlaps in expression with *ZmCLE7* in the L1 layer of the IM. Consistent with this, CT2 interacts with FEA2 and suppresses SAM growth through ZmCLE7 signaling (Bommert et al. 2013a; Je et al. 2018). Maize also encodes three non-canonical G alpha subunits, extra-large GTP binding proteins (*ZmXLG1*, *ZmXLG3a*, and *ZmXLG3b*), which function redundantly with CT2 in controlling SAM development (Wu et al. 2018a). Interestingly, all *Zmxlg* triple mutant is seedling lethal due to over-activation of the immune system (Wu et al. 2018a). Maize *G protein beta subunit gene1* (*ZmGβ1*) also functions downstream of *FEA2* (Wu et al. 2020). The *Zmgβ1*^{CR} knockout mutant also causes seedling lethality, whereas a weak allele *Zmgβ1*^{D277N} has enlarged IMs and fasciated ears (Wu et al. 2020). *ZmCORYNE* (*CRN*) encodes a transmembrane pseudokinase, and also interacts with FEA2, as in *Arabidopsis*, and inhibits SAM growth through maize *FON2-LIKE CLE PROTEIN1* (*ZmFCP1*) signaling (Muller et al. 2008; Je et al. 2018). However, CT2 and ZmCRN do not interact with each other, even though FEA2 interacts individually with CT2 or ZmCRN (Je et al. 2018), suggesting that the specificity of FEA2 for different signals is achieved by specific downstream effectors. In fact, FEA2/CLV2 appears to transduce several CLEs signals (Fiers et al. 2005; Meng and Feldman 2010; Hazak et al. 2017) and interacts with various LRR-RLPs in multiple roles (Somssich et al. 2016), suggesting that CLV2/FEA2 is a hub of CLE signaling pathways. However, CLV2/FEA2 does not directly interact with CLE peptides (Somssich et al. 2016; Shinohara and Matsubayashi 2015), indicating that they require unknown co-receptors to perceive CLE peptide signals. The expression of *FEA2* is not restricted to the SAM (Taguchi-Shiobara et al. 2001), suggesting that CLV2/FEA2 play multiple roles. CLV2 also appears to be involved in biotic interactions (Replogle et al. 2011; Hanemian et al. 2016) as well as autoimmune signaling (Wu et al. 2020, 2018a).

Given that canonical CLV-WUS signaling pathway mostly involves communication between CZ and OC domains within the SAM, it does not explain the balance between stem cell proliferation and ongoing cellular differentiation in the PZ for lateral organ formation (Nardmann et al. 2016; Strable and Scanlon 2016). Feedback signals from organ primordia to the stem cell niche have been proposed to compensate for the defects of communication between stem cell niche and the differentiated descendants (Goldshmidt et al. 2008). *FASCIATED EAR3* (*FEA3*) in maize encodes an LRR receptor-like protein and negatively regulates SAM growth (Je et al. 2016), like CLV signaling. However, *FEA3* is expressed in the OC and RZ. *fea3* mutants do not respond to ZmCLE7 peptide, but do respond to ZmFCP1, which is expressed in the PZ and leaf primordia. Interestingly, *FEA3-ZmFCP1* signaling restricts *ZmWUS1* expression to the OC by excluding it from the RZ (Je et al. 2016), suggesting that *FEA3-ZmFCP1* signaling is involved in communication between differentiated descendants of stem cells and the stem cell niche.

Transcriptional Regulation

Recently, dominant *Barren inflorescence3* (*Bif3*) mutants were found to harbor a tandem duplicated copy of *ZmWUS1*, producing a ring-like pattern of *ZmWUS1* overexpression in the IM due to a novel chimeric promoter, and enlarged SAM and IM (Chen et al. 2021). However, the *Bif3* ring-like pattern of *ZmWUS1* expression in IM disappeared in the *fea3* mutant background (Chen et al. 2021), indicating this pattern is related to inhibition by FEA3 in the RZ. Interestingly, the enlarged IMs of *Bif3* mutants do not produce typical fasciated ears, but rather small, ball-like ears with few SMs (Chen et al. 2021), suggesting that *ZmWUS1* overexpression inhibits the differentiation of axillary organs. Like *ZmWUS1*, the homeodomain transcription factor KNOTTED1 (KN1) acts non-cell-autonomously to activate meristematic fate (Jackson et al. 1994; Lucas et al. 1995; Kim et al. 2005; Song et al. 2020), as *kn1* loss-of-function mutants exhibit smaller SAMs (Kerstetter et al. 1997; Vollbrecht et al. 2000). *YABBY* transcription factors *DROOPING LEAF1* (*DRL1*) and *DRL2*, which are exclusively expressed in leaf primordia, also appear to promote stem cell fate, as the *drl1;drl2* double mutants have smaller SAMs (Strable et al. 2017), suggesting that *DRL1* and *DRL2* are also involved in communication between SAMs and the differentiated descendants of stem cells. However, *DRL1* and *DRL2* seem to be involved in positive feedback signaling. Consistent with this speculation, duplicate copies of two transcription factor genes, MADS-box gene *Zmm8* and YABBY gene *DRL2*, at the *Fascicled ear1* (*Fas1*) locus, are ectopically overexpressed in the CZ of the IM (Du et al. 2021), leading to an enlarged IM. In addition to these positive stem cell

regulators, the *bZIP* transcription factor *FEA4* is a negative stem cell regulator and a *PERIANTHIA* ortholog in maize (Pautler et al. 2015). *FEA4* is expressed in the PZ of the vegetative SAM and throughout the entire IM, and *fea4* mutants exhibit enlarged vegetative SAMs and fasciated IMs. FEA4 interacts with the redox protein MALE STERILE CONVERTED ANTHER1 (MSCA1)/ABPHYL2 (Yang et al., 2015), suggesting that it promotes lateral organ differentiation in the PZ of the SAM. *SQUAMOSA PROMOTER BINDING* (*SBP)-box* transcription factor genes *unbranched2* (*ub2*) and *ub3* are expressed in the meristem PZ to control inflorescence development (Du et al. 2020; Chuck et al. 2014). These transcription factors are targeted by miRNA156 (Chuck et al. 2010; Wu and Poethig 2006). Two tandem microRNA156 (miR156) are overexpressed in the IM and the lateral organs in *Cg1* mutants, which produce fasciated tassels (Chuck et al. 2007a). miRNA biogenesis requires the RNA endonuclease DICER-LIKE1 (Kurihara and Watanabe 2004). In maize, *FUZZY TASSEL (FZT)* encodes a *DICER-LIKE1* homolog and mutants have inflorescence defects including IM fasciation and severely reduced plant height and shorter, narrower leaves, due to reduced level of miRNAs associated with meristem determinacy, phase change and leaf polarity (Thompson et al. 2014). Similar phenotypes are found in mutants of the transcriptional coactivator *grf-interacting factor1* (*gif1*), which is expressed in leaf primordia, PZ, and RZ of the SAM and IM, but not in the CZ (Zhang et al. 2018; Kim and Kende 2004). Most of the mutants in transcriptional regulation genes also have strong defects in tassel development.

Conclusions and Perspectives

Fasciation patterns are very important for genetic analysis as well as improving crop yields (Fig. 4A–F). However, depending on genetic background or environment, these patterns can be modified. For example, cooler and lower light conditions alleviate fasciation phenotype, as do some genetic backgrounds with smaller IMs, such as Mo17 (Bommert et al. 2013b). Fasciation phenotypes can also be synergistically enhanced in some genetic backgrounds (Yu et al. 2008), providing an opportunity to identify further genetic components. Some weaker mutants have mild flattened IMs without fasciation, whereas stronger mutants exhibit specific patterns of fasciation, such as line or ring fasciation or even IM bifurcation (Fig. 4B–F). This common phenomenon and recent gene-editing techniques open the door to a potential that any mutant with fasciation can help improve crop yields.

However, we are faced with some interesting questions to address.

Why cannot strong alleles be used to improve yield?

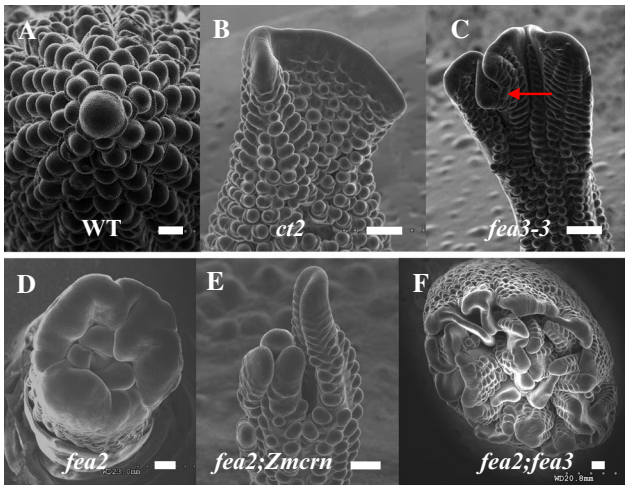

Fig. 4 Strong mutants exhibit specific patterns of fasciation. **A** Wild-type ear IM shows a dome-shaped apex. **B** *ct2* shows the typical ridge-like line pattern of IM. **C** IM bifurcation often occurs in the line pattern of ear. Red arrow indicates IM bifurcation. **D** Ring pattern of IM is often observed in *fea2* mutants. **E** The ring pattern of the IM often gives rise to the radial bifurcation of the IM. **F** Synergistically enhanced fasciation of *fea2;fea3* double mutant exhibits a highly enlarged ring pattern of IM with many small ears. Scale bars: 200 μm

Most strong fasciation mutants with extreme KRN increases have stunted ears with poor yield. To address this issue, weak alleles have been used (Bommert et al. 2013b; Je et al. 2016; Liu et al. 2021a). Why strong fasciation mutations reduce ear length has not been clearly studied. It is speculated that the limited amount of nutrients provided by the source organs may be key signal controlling ear development. In contrast, strong fasciation in tomatoes can increase the size of fruit with increased locule numbers (Rodriguez-Leal et al. 2017), suggesting that strong fasciation can be very useful for other species.

Can IM regulators promote source organ development?

For yield improvement, sink organ improvement alone is meaningless without joint improvement of photosynthetic source capacity. A weak allele of *fea3* increased overall yield, suggesting that *FEA3-FCP1* signaling impacts sink–source relationships (Je et al. 2016; Kitagawa and Jackson 2019). *ZmFCP1* overexpression shows has a negative effect on seedling growth, suggesting this gene controls vegetative development and SAM size regulation. *ct2* mutants also have defects in leaf development (Bommert et al. 2013a). However, the functions of ZmFCP1 and ZmCLE7 in vegetative growth have not been carefully dissected. In addition, the transcriptional IM regulators, *Cg1*, *fzt*, *gif1*, and *fea4* also have vegetative growth defects, suggesting that the growth balance between sink and source organ development may involve IM regulators. Therefore, a better understanding of the function of IM regulators in sink–source balance in plant development may lead to higher yield improvements.

Which players regulate IM bifurcation?

Bifurcation and branching of IMs (Fig. 4C, E) are important traits for improving plant yields. Patterns of fasciation vary depending on the pathway. Generally, *Zmcle7*-related mutants show a ridge or ring fasciation (Fig. 4B, D), whereas *Zmfcp1*-related mutants often have ear bifurcation (Fig. 4C, F). This trend appears to be conserved in *Arabidopsis*, as *clv1*, *clv2*, and *clv3* show little IM bifurcation (*****Clark et al. 1993, 1995, 1997; Kayes and Clark 1998; Jeong et al. 1999; Fletcher et al. 1999), whereas *Atfea3* mutants develop reiterative IM bifurcation (Je et al. 2016). A model of *Fas1* action suggests that misexpression of *Zmm8* and *drl2* in the CZ of the IM suppresses its meristematic activity and promotes meristematic activity in the PZ, resulting in repeatedly bifurcated inflorescences. Consistently, IM bifurcation appears in mutants of *fea3*, *fea4*, *Zmcrn*, *ub2;ub3*, *gif1*, and *td1*, and all these genes are expressed in the PZ or the RZ of vegetative SAMs, but not in from the CZ, suggesting that these genes also promote meristematic activity of the PZ. However, further studies are needed to understand the detailed mechanisms of IM bifurcation.

Are other CLE peptides involved in IM regulation?

Among 49 *CLE* genes in maize, only *ZmCLE7*, *ZmFCP1*, and *ZmCLE1e5* have been characterized. *Zmcle7* and *Zmfcp1* mutants develop fasciated ears, and *Zmcle1e5* enhances the fasciation phenotype of *Zmcle7* (Liu et al. 2021a). However, the others remain uncharacterized, even though many are expressed in shoot tissues (Goad et al. 2017). In addition, other peptides classes may be involved in IM regulation.

How to explain the mysterious ear transformation during domestication?

Many domestication-associated genes in maize have been identified and described with respect to improved traits such as lack of shattering, reduction of tillering and lateral branching, and reduction of glumes and cupules (Dong et al. 2019; Stitzer and Ross-Ibarra 2018). However, a clear explanation of the mysterious transformation of the ear inflorescence phyllotaxy is not yet available. It is believed that domestication of ear rank occurred slowly over > 5000 years before the present (Benz 2001). Interestingly, the prolificacy domestication trait, related to the number of ears on a shank, is controlled by IM size regulators, including G protein alpha subunit *ct2* and *gif1* that suppress axillary ear formation (Urano et al. 2015; Zhang et al. 2018). These observations suggest that fasciation mutants are involved deeply in maize domestication.

Although the genes involved in domestication and inflorescence architecture appear to be conserved in diverse plant species (Dong et al. 2019; Kitagawa and Jackson 2019; Liu et al. 2021b), the ear architecture of maize is unique in grain crops. The further understanding of maize inflorescence architecture could help improve yields in maize and other crops.

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Declarations

Conflict of interest The authors declare that they have no competing interests.

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Consent for Publication All the authors have provided consent for publication.

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