



Plant Inflorescence Architecture: The Formation, Activity, and Fate of Axillary Meristems

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The above-ground plant body in different plant species can have very distinct forms or architectures that arise by recurrent redeployment of a finite set of building blocks—leaves with axillary meristems, stems or branches, and flowers. The unique architectures of plant inflorescences in different plant families and species, on which this review focuses, determine the reproductive success and yield of wild and cultivated plants. Major contributors to the inflorescence architecture are the activity and developmental trajectories adopted by axillary meristems, which determine the degree of branching and the number of flowers formed. Recent advances in genetic and molecular analyses in diverse flowering plants have uncovered both common regulatory principles and unique players and/or regulatory interactions that underlie inflorescence architecture. Modulating activity of these regulators has already led to yield increases in the field. Additional insight into the underlying regulatory interactions and principles will not only uncover how their rewiring resulted in altered plant form, but will also enhance efforts at optimizing plant architecture in desirable ways in crop species.

The colonization and radiation of plants on land was a major event in plant evolution, shaping the terrestrial biosphere and the geosphere and transforming global climate. The embryophytes, informally named land plants, originated around 430 million years ago from the last shared unicellular ancestor classified among the charophyta, a group of freshwater green algae (Wickett et al. 2014; Jill Harrison 2017). Evolution from the aquatic to the terrestrial habitat of plants required key morphological innovations (Pires and Dolan 2012). Based on recent molecular phylogenetic advances, comparative analysis pinpoints fundamental body plan features in plant evolution, such as multicellularity, plasmodesmatal cell–cell connec-

tions, specialized apical cell fates, three-dimensional apical growth, asymmetric cell division, bifurcation, diversification of indeterminate branched forms with leaves and roots, as well as axillary branching (Wang and Li 2008). Those innovations in development and the underlying genetic changes drive the radiation of the three-dimensional organization of the plant body and, thus, plant architecture (Reinhardt and Kuhlemeier 2002).

Plant architecture is a product of development and keeps changing during the life cycle of plants from young seedlings to adult plants. Plant architecture furthermore is species specific and it has long been the best means of identifying plants (Yang and Hwa 2008). The architec-

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ture of a plant is also influenced by environmental conditions such as light, temperature, humidity, and nutrient status (Harder and Prusinkiewicz 2012; Morris et al. 2017; Scheres and van der Putten 2017). Based on plant molecular and genetic studies, the equilibrium between endogenous and exogenous cues define the relative arrangement of above-ground parts of the plant, including the branching pattern (the degree of branching and internodal elongation) and shoot determinacy (the size, shape, and position of leaves, branches, and flowers). Above-ground plant architecture is thus a collection of important agronomic traits and a major determinant of ability of plants to thrive during cultivation, their yield and quality, and harvesting efficiency (Wang et al. 2018). During reproductive development, the inflorescence architecture can be determinate (i.e., terminate in a flower) or indeterminate; simple (flowers are borne on the main stem) or compound (flowers born on branches). For example, *Arabidopsis* and snapdragon form indeterminate simple inflorescences, whereas pea and *Medicago* have determinate compound inflorescences. The inflorescences of tomato are determinate and compound; while maize and rice have determinate or indeterminate compound inflorescences, respectively (Benlloch et al. 2015; Bommert and Whipple 2018). Recent advances in our understanding of the molecular-genetic regulation of plant architecture are mostly from these and other model and crop plants (Benlloch et al. 2007; Zhang and Yuan 2014; Teichmann and Muhr 2015; Bommert and Whipple 2018; Chongloi et al. 2019) and have begun to shed light on how individual aspects of plant architecture initiate, develop, and are maintained. This review will focus on these advances and the underlying genetic determinants.

LATERAL ORGAN INITIATION

Lateral organs initiate from the flanks of the stem cell pool containing shoot apical meristem (SAM) at sites of local auxin maxima (Weijers and Wagner 2016). Stem cell descendants in the SAM periphery can respond to auxin maxima by initiating primordia and so-called axillary mer-

istems; the latter in turn can be dormant, or grow out and become branches or flowers (Prusinkiewicz et al. 2007; Martín-Fontecha et al. 2018). The phyllotaxis—the species-specific arrangement of the lateral organs along the stem and inflorescence—relies on the positioning of auxin maxima together with additional chemical (cytokinin) and physical (mechanical) cues (Kuhlemeier 2017; Truskina and Vernoux 2018; Shi and Vernoux 2019).

Recent advances have shed light on the transcriptional responses triggered by auxin sensing that enable formation of lateral organ primordia. In reproductive meristems of *Arabidopsis*, the auxin signal is primarily transduced by the auxin response factor (ARF) MONOPTEROS (MP) (Vernoux et al. 2010; Weijers and Wagner 2016). MP directs initiation of reproductive primordia in part by up-regulating expression of diverse transcription factors, including the YABBY transcription factor FILAMENTOUS FLOWERS (FIL), the LEAFY (LFY) transcription factor, important for floral fate, and two PLETHORA transcription factors that promote organ growth (Yamaguchi et al. 2013; Wu et al. 2015). Auxin-dependent up-regulation of *FIL* and *LFY* depends on recruitment of chromatin remodelers that open up chromatin near MP-bound sites at target loci (Wu et al. 2015). More recently, two additional ARFs [ETTIN (ETT) and ARF4] were shown to promote lateral organ initiation in parallel with MP and sever *mp ett arf4* triple mutants fail to initiate any lateral organs. MP, ETT, and ARF4 jointly promote organogenesis by down-regulating the expression of class I KNOX pluripotency genes (*SHOOT MERISTEMLESS* [*STM*] and *BREVIPEDICELLUS* [*BP*]). MP represses class I KNOX genes indirectly, via its direct target *FIL*, whereas ETT/ARF4 repress these genes directly. *STM*/*BP* repression by the YABBY/ARF complex is mediated by chromatin compaction through histone deacetylation (Chung et al. 2019). Subsequent to flower initiation, *STM* is up-regulated when the flower meristem is established in stage 2 flowers by an as-yet unknown mechanism. In addition, *STM* is up-regulated in the boundary between the initiating flower and the meristem by mechanical signals, which enables separation of



the primordium from the meristem (Landrein et al. 2015).

In inflorescences, on the basis of live imaging and reporter constructs, the auxin-positive (and *STM*-depleted) region comprises both the cryptic bract and the cells that give rise to the flower (Heisler et al. 2005). Burian et al. (2016) recently provided evidence that axillary meristems that give rise to branches form at sites where auxin response is high concomitant with leaf initiation, as do flowers. These studies focused on secondary branches that arise in the axils of bracts (also called cauline leaves) early during reproductive development (40-day-old short-day grown plants). The combined studies from *Arabidopsis* and tomato suggest similarities between initiation of bracts with associated secondary branches and flowers plus (cryptic) bracts during reproductive development.

Axillary meristem initiation during vegetative development is delayed relative to leaf initiation and requires an auxin minimum that supports low *STM* expression (Wang et al. 2014; Zhou et al. 2014; Shi et al. 2016). Thus, during vegetative development, lateral organ initiation and branch meristem formation are distinct events with opposite auxin requirements, which will be discussed further below.

The role of auxin and cytokinin in lateral organ initiation during reproductive development is evolutionarily conserved in the grasses (for reviews, see Barazesh and McSteen 2008; Matthes et al. 2018). In both maize and rice inflorescences, auxin and PIN markers reveal auxin accumulation in primordia that will give rise to branches, spikelets, spikelet pairs (maize), and flowers with associated (cryptic) bracts or leaves (Gallavotti et al. 2008; Galli et al. 2015; Yang et al. 2017). Likely because of genetic redundancy, specific ARFs have thus far not been linked to auxin-mediated lateral organ initiation (Galli et al. 2015). However, mutations in two Aux/IAA proteins—negative regulators of ARFs like MP—caused defects in lateral organ initiation in male and female inflorescences in maize (Galli et al. 2015). The identified Aux/IAA auxin response inhibitors act directly upstream of a classical regulator of lateral organ initiation, the bHLH transcription factor BARREN STALK1

(BA1) (Gallavotti et al. 2004). The BA1 homolog in rice, LAX PANICLE 1 (LAX1) also promotes initiation of lateral organs (Komatsu et al. 2003). In maize and rice, similar BA1/LAX1 interacting nuclear proteins with putative RAWUL/PDZ/SH3 domains called BA2 (Yao et al. 2019) or LAX2 (Tabuchi et al. 2011) were identified. LAX2 links to auxin response in other processes by blocking the interaction between Aux/IAA proteins and ARFs (Li et al. 2018). Mutants in the *Arabidopsis* BA1/LAX1 homolog ROX display defects in initiation of meristems in the axils of leaves during vegetative development (Yang et al. 2012). A role for YABBY family members in lateral organ initiation, as described above for *Arabidopsis*, is conserved in rice; simultaneous loss- or reduction-of-function in three FIL YABBY proteins leads in the most extreme cases to formation of naked inflorescence branches lacking spikelets (Tanaka et al. 2017).

In the remainder of this review, we will consider the different developmental trajectories of the axillary meristems, which we define here as populations of cells born in the axils of leaves initiated either concomitantly with leaves or much later, which have the potential to give rise to leaves, branches, and flowers. Taking recent research into account, this review will focus on mechanisms underlying axillary meristem formation, activity, and identity as major contributors to plant architecture and to agronomically desirable plant traits.

AXILLARY MERISTEM INITIATION

As outlined above, axillary meristem initiation and development during vegetative development is delayed relative to leaf initiation and furthermore regulated by transcriptional regulators largely conserved between eudicots and monocots (Teichmann and Muhr 2015; Wang and Jiao 2018).

The combined available data suggest that in eudicots (*Arabidopsis*/tomato) and monocots (rice) a cascade of transcription factors coordinately up-regulate the pluripotency gene *STM* to enable formation of the axillary meristem (e.g., see Tian et al. 2014; Tanaka et al. 2015). The *Lateral suppressor* (*Ls*) gene of tomato encodes

a member of the VHIID subfamily of the plant-specific GRAS (GA INSENSITIVE, REPRESSOR OF GA1-3, SCARECROW) transcription factor that is required for axillary meristem initiation in many plant species besides tomato, such as *Arabidopsis* *LATERAL SUPPRESSOR* (*LAS*) and rice *MONOCLUM1* (*MOC1*) (Greb et al. 2003; Li et al. 2003). The *las* mutant is unable to form lateral shoots and the *moc1* mutant has a single primary stem (culm) lacking tillers during vegetative development (Greb et al. 2003; Li et al. 2003). *MOC1* in rice and TaMOC1 in wheat also play a role in inflorescence branching (Li et al. 2003; Zhang et al. 2015).

The tomato *Blind* (*Bl*) gene encodes an R2R3 class MYB transcription factor and is required for axillary meristem initiation. During vegetative development, *bl* mutants lack axillary meristems in most leaves (Schmitz et al. 2002). Likewise, *Arabidopsis* *REGULATORS OF AXILLARY MERISTEM* (*RAX*) genes, homologs of *Bl*, control axillary meristem initiation. *RAX1/MYB37*, *RAX2/MYB38*, and *RAX3/MYB84* act redundantly in this process (Müller et al. 2006). *RAX1* acts in parallel with *LAS* in axillary meristem initiation and both genes promote establishment/maintenance of *STM* expression in axillary meristems (Greb et al. 2003; Keller et al. 2006; Müller et al. 2006). *RAX* proteins have additional roles during reproductive development (Keller et al. 2006; Müller et al. 2006). Recently, gain-of-function of five closely related WRKY transcription factors each promoted axillary meristem initiation; one of these, *EXCESSIVE BRANCHES1* (*EXB1/WRKY71*), positively regulates *RAX1*, 2, and 3 transcription (Guo et al. 2015).

The class III HD-ZIP transcription factor *REVOLUTA* (*REV*) and the AP2 transcription factor *DORNROESCHEN* (*DRN*) also contribute to axillary meristem initiation during vegetative development (Shi et al. 2016; Zhang et al. 2018). The *drn drnl* double mutant fails to initiate lateral meristems, whereas *REV* and *DRN* together promote *STM* up-regulation. Some genes affecting axillary meristem initiation, such as *RAX1* and *Bl*, up-regulate *CUP-SHAPED COTYLEDON 1* (*CUC1*), *CUC2*, and *CUC3*, and these

NAC transcription factors redundantly promote axillary meristem initiation (Hibara et al. 2006; Raman et al. 2008). A recent study of mobile and nonmobile *STM* function revealed that *STM* mobility is critically important to suppress axillary meristem formation by precisely regulating *CUC* genes (Balkunde et al. 2017). Up-regulation of *STM* during vegetative axillary meristem initiation is also important in other plant species. In rice, *TILLERS ABSENT1* (*TAB1*), a *WUSCHEL* ortholog promotes formation of the axillary meristem via the activation of *OSH1*, the meristematic cells marker and the ortholog of *STM* (Lu et al. 2015; Tanaka et al. 2015).

AXILLARY MERISTEM OUTGROWTH

Transcriptional Control of Axillary Meristem Outgrowth

Vegetative axillary meristems, once initiated, either grow out as branches or form dormant axillary buds. Thus, the final number of branches is determined by the number of axillary meristems formed, the activity of the axillary buds, and the timing of flower formation. Endogenous cues related to developmental stage and meristem activity at the main shoot are integrated with environmental signals related to nutrient status or plant density to optimize bud outgrowth for plant survival and fitness (Domagalska and Leyser 2011). For example, to survive under adverse conditions, axillary meristems can switch to a dormant state. Once environmental or endogenous conditions change, dormant organs can resume growing (Martín-Fon-techa et al. 2018).

In many plant species, TCP transcription factors promote bud dormancy. Maize *TEOSINTE BRANCHED 1* (*TB1*) encodes a class II TCP family transcriptional regulator expressed in axillary buds and axillary branches and prevents bud outgrowth (Doebley et al. 1997; Hubbard et al. 2002). The *TB1* homologs *Arabidopsis* *BRANCHED1* (*BRC1*) (Aguilar-Martínez et al. 2007; Seale et al. 2017), rice *FINE CULM1* (*FC1/OsTB1*) (Minakuchi et al. 2010), sorghum (*Sorghum bicolor*) *SbTB1* (Kebrom et al. 2006) and *Tulipa gesneriana* (*TgTB1*)

(Moreno-Pachon et al. 2018) are also expressed in axillary meristems and buds and prevent their outgrowth. Both TB1 in maize and BRC1 in *Arabidopsis* also affect onset of flower formation in branches (Hubbard et al. 2002; Niwa et al. 2013). A recent study in *Arabidopsis* shows that buds in which *BRC1* has accumulated can be activated, indicating that *BRC1* is not sufficient for bud growth inhibition (Seale et al. 2017).

Transcriptomes of active and dormant axillary buds in herbaceous and woody plant species have identified additional regulators of bud activity (Stafstrom et al. 1998; Tatematsu et al. 2005; Wood et al. 2013; Kebrom and Mullet 2016). These studies point to a small disordered protein of unknown function called dormancy marker gene *DORMANCY ASSOCIATED PROTEIN 1* (*DRM1*) expressed specifically in dormant axillary buds of pea (Stafstrom et al. 1998), *Arabidopsis* (Tatematsu et al. 2005), wheat (Kebrom et al. 2012), sorghum (Kebrom et al. 2006), kiwifruit (Wood et al. 2013), and poplar and grapevine (Tarancón et al. 2017).

Systemic Control of Axillary Meristem Outgrowth

Multiple signals modulate outgrowth of dormant axillary buds, such as phytohormones (auxin, cytokinin, strigolactones, and abscisic acid [ABA]), nutrients (sugars, nitrogen), light quality (far red), and damage to the shoot apex (decapitation) (Fig. 1; Domagalska and Leyser 2011).

Auxin produced in the shoot enters the rootward polar auxin transport (PAT) stream and prevents bud outgrowth in at least two ways: by modulating production of cytokinin and strigolactone, which act in the axillary buds (Dun et al. 2012; Teichmann and Muhr 2015; Dierck et al. 2016), and by regulating auxin flow out of buds (Sachs 1981; Prusinkiewicz et al. 2009; Balla et al. 2011). The latter response is less pronounced in pea (Chabikwa et al. 2019). Auxin represses the biosynthesis of cytokinins, which promote bud outgrowth, via down-regulation of ADENYLATE ISOPENTENYLTRANSFERASE (IPT)

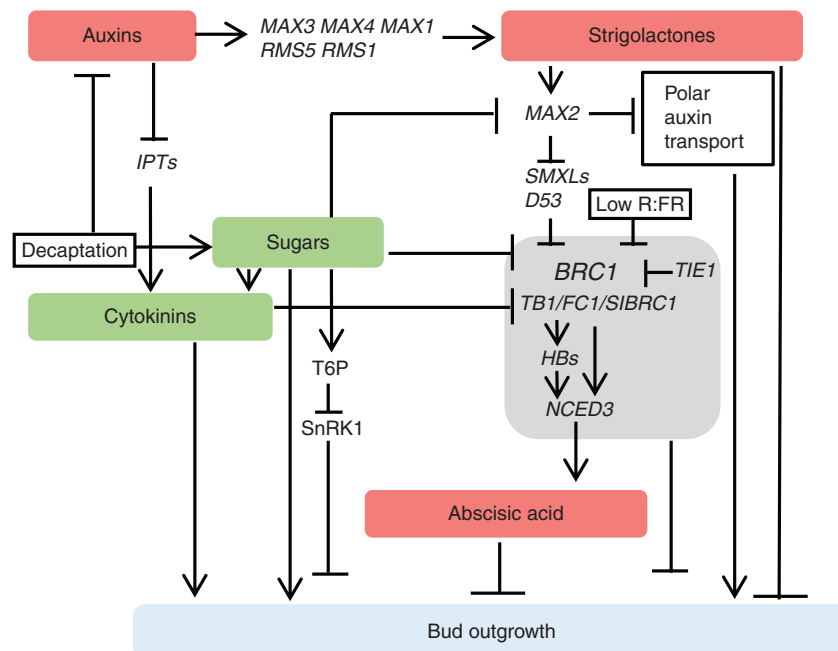


Figure 1. Phytohormones, sugars, and key regulatory genes control bud outgrowth. Different types of phytohormones (auxin, cytokinin, strigolactone, and abscisic acid) as well as sugars are key endogenous determinants of bud outgrowth. The complex interplay among those regulatory pathways are summarized (see text for details).



family members in the nodal stem (Tanaka et al. 2006). Auxin promotes synthesis of strigolactone, which inhibits bud outgrowth via up-regulating *MORE AXILLARY GROWTH 3* (*MAX3*) and *MAX4* expression (Hayward et al. 2009). Recently, the highly branched *rms2* mutant of pea, which has lower levels of strigolactone, was shown to be caused by a defect in an ABF4/5 like auxin receptor (Ligerot et al. 2017).

Cytokinins can directly promote bud outgrowth regardless of auxin accumulation (Sachs and Thimann 1967; Müller et al. 2015). Cytokinins are mostly synthesized in the root but also locally in the shoot and are transported shootward in the xylem (Chen et al. 1985). How cytokinin promotes bud outgrowth is still not fully understood. Cytokinin inhibits accumulation of *BRC1* in pea and *Arabidopsis* (Braun et al. 2012; Dun et al. 2012; Seale et al. 2017). In addition, cytokinin enhances polar auxin transport in the main stem by promoting accumulation of the polar auxin efflux regulators, PIN3, 4, and 7 (Waldie and Leyser 2018). Cytokinin response regulators also contribute to dormancy; with “repressive” type-A cytokinin response regulators (ARRs) promoting and “activating” type-B ARR inhibiting bud outgrowth in *Arabidopsis* (Müller et al. 2015; Waldie and Leyser 2018). The molecular mechanism for this is not yet understood, but it has been proposed that the phenotypes of the cytokinin response regulator mutants may be attributable to their effects on cytokinin homeostasis (Waldie and Leyser 2018).

The hormone strigolactone inhibits branch outgrowth in *Arabidopsis*, pea, rice and petunia (for reviews, see Domagalska and Leyser 2011; Barbier et al. 2019). The available evidence suggests that strigolactones prevent bud outgrowth at least in part by up-regulating expression *BRC1* (Dun et al. 2012) and by impacting auxin transport (see below). Strigolactone, received by *Arabidopsis* and rice *DWARF14* (*D14*) (Chevalier et al. 2014), leads to degradation of strigolactone response regulators mediated by the F-box protein *MAX2* in *Arabidopsis* and the homolog *D3* in rice (Jiang et al. 2013; Zhou et al. 2013). Strigolactone response regulators important for branch outgrowth include the *SUPPRESSOR OF MAX2 1-LIKE* (*SMXL*) 6, 7, and 8 genes in

Arabidopsis and co-ortholog *DWARF53* (*D53*) in rice (Jiang et al. 2013; Zhou et al. 2013; Soundappan et al. 2015; Wang et al. 2015b). *smxl* 6, 7, and 8 can restore branch suppression in strigolactone biosynthesis and signaling mutants (Soundappan et al. 2015; Wang et al. 2015b). *D53*-like *SMXLs* promote branching by down-regulating *BRC1* (Seale et al. 2017). However, this does not explain all of strigolactone action as buds in *brc1 brc2* double mutant are strigolactone responsive (Seale et al. 2017). *FC1/OsTBI* functions downstream of strigolactones to inhibit the outgrowth of buds (Minakuchi et al. 2010). The pea *Psbrc1* mutant displays an increased shoot-branching phenotype, is able to synthesize strigolactone, and does not respond to strigolactone application (Braun et al. 2012). Tomato *SIBRC1a* and *SIBRC1b* are expressed in arrested axillary buds and both are down-regulated on bud activation (Martín-Trillo et al. 2011).

Strigolactone also negatively regulates auxin flux and PIN1 polarization via the *max* pathway (Bennett and Leyser 2006; Bennett et al. 2006, 2016) and promotes rapid PIN1 endocytosis (Crawford et al. 2010; Shinohara et al. 2013; Xu et al. 2015). Indeed, branching defects of strigolactone biosynthesis mutants can be rescued by inhibition of PAT (Bennett and Leyser 2006; Bennett et al. 2006). Strigolactone can also inhibit branching independent of auxin (Brewer et al. 2009, 2015; Chabikwa et al. 2019).

Sugar promotes bud outgrowth and it has been suggested that the growing shoot tip may suppress branch outgrowth because it acts as a sugar sink (Barbier et al. 2015b; Kebrom 2017). Addition of sucrose to inhibited buds can rapidly release inhibition by repressing *BRC1* expression (Mason et al. 2014). Studies on shoot branching in barley (Felippe and Dale 1973), sorghum (Kebrom and Mullet 2015), wheat (Kebrom et al. 2012), rose (Barbier et al. 2015a), and *Arabidopsis* (Otori et al. 2017) have also indicated a strong association between sucrose supply and axillary bud outgrowth. The rice *monoculm* mutant *moc2*, which is defective in branch outgrowth and has significantly reduced tiller numbers, displays reduced sucrose supply to the buds and is caused by disruption of cytosolic fructose-1,6-

bisphosphatase 1 (*FBP1*) gene (Koumoto et al. 2013). Recent studies suggest that sucrose may act as a signal rather than an energy substrate in promoting bud outgrowth (Barbier et al. 2015b). Overexpression of *Arabidopsis* HEXOKINASE1 (*HXK1*) leads to the increased number of primary rosette branches, increased expression of ABA-related genes, and reduced expression of auxin-related genes (Kelly et al. 2012). Trehalose-6-P (T6P) accumulates to low concentrations in wild-type plants (Grennan 2007). Loss of activity in the *Arabidopsis* trehalose-6-P synthase 6 (*TPS6*), which encodes an active trehalose synthase (Chary et al. 2008), leads to reduced bud outgrowth (Schluepmann et al. 2003; Chary et al. 2008). In addition, T6P levels in the axillary buds of pea increase rapidly after decapitation, triggering onset of bud outgrowth (Fichtner et al. 2017). More importantly, signaling of carbon and nitrogen metabolic pathways might be integrated at the level of T6P to control axillary meristem outgrowth (Fichtner et al. 2017; Barbier et al. 2019). It has been proposed that T6P may link to carbon starvation syndrome, and genes related to this pathway are enriched in dormant buds of poplar and grapevine (Tarancón et al. 2017).

Little is known about hormonal control inside axillary buds during the growth-to-dormancy transition, although ABA accumulation may promote bud dormancy (Reddy et al. 2013; Yao and Finlayson 2015). ABA was proposed to be a general inhibitor of axillary bud outgrowth (Shimizu-Sato and Mori 2001; Yao and Finlayson 2015). *BRC1* stimulates the ABA biosynthesis pathway by the up-regulation of *HOMEODOMAIN PROTEIN 21* (*HB21*), *HB40*, and *HB53*, which in turn activate the ABA biosynthesis gene *NINE-CIS-EPOXICAROTENOID DIOXYGENASE 3* (*NCED3*) (González-Grandío et al. 2017). TCP interactor containing EAR motif protein 1 (*TIE1*) interacts with *BRC1* and prevents it from activating *HB21*, *HB40*, and *HB53* expression (Yang et al. 2018). ABA levels increase in buds under low R/FR light and in phytochrome B mutants, which also display reduced branch outgrowth in Sorghum and *Arabidopsis* (Kebrom et al. 2010; Reddy et al. 2013; Yao and Finlayson 2015; Kebrom and Mullet 2016). This

may be a response to plant density/shade avoidance.

AXILLARY MERISTEM IDENTITY IN THE INFLORESCENCE

Axillary Meristems that Remain Vegetative

Axillary meristems in the inflorescence can adopt a variety of different fates: They can remain vegetative, give rise to branches, or become flowers. During the vegetative-to-reproductive transition in axillary meristems, plants integrate environmental and developmental stimuli and either “decide” to irreversibly initiate reproductive development—give rise to flowering branches or flowers (most *Arabidopsis* cultivars)—or remain vegetative, as do a subset of axillary meristems in perennial species.

In *Arabidopsis*, vegetative meristems can form aerial rosettes in lieu of flowering branches. This is in all cases linked with a severe delay in the onset of reproductive development, triggered by gain-of-function of flowering repressors or by loss-of-function of flowering activators. For example, in annual *Arabidopsis thaliana* accession (Columbia-0), overexpressing the mobile “antiflorigen” *TERMINAL FLOWER 1* (*TFL1*) in non-inductive photoperiod (short-day) not only severely delays onset of reproduction but produces large aerial rosettes (Ratcliffe et al. 1998). Consistent with its opposite role to *TFL1*, failure to fully induce *FLOWERING LOCUS T* (*FT*) also leads to formation of aerial rosettes (Liu et al. 2014). Mutations in two flowering activator MADS box transcription factors, *SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1* (*SOC1*) and *FRUITFULL* (*FUL*) *soc1 ful* double mutants, form many aerial rosettes even in inductive photoperiod and resemble perennial plants (Melzer et al. 2008). Aerial rosette formation in the late flowering Sy-0 accession of *Arabidopsis* has been attributed to elevated levels of the flowering repressor *FLOWERING LOCUS C* (*FLC*), a known negative regulator of the mobile florigen *FT* (Wang et al. 2007).

These phenotypes are reminiscent of vegetative meristems in the perennial species *Arabis*



alpina. The *FLC* ortholog *PERPETUAL FLOWERING 1 (PEP1)*, the *AP2* ortholog *PEP2*, *TFL1*, and *miR156* promote the perennial growth habit, in which some axillary meristems remain vegetative (Wang et al. 2009, 2011; Bergonzi et al. 2013; Lazaro et al. 2018, 2019; Hyun et al. 2019). After vernalization, *PEP1* represses flowering branch or flower formation in these axillary meristems (Wang et al. 2009; Lazaro et al. 2018) in a mechanism that is partially dependent on *PEP2* (Lazaro et al. 2019). Plant mutants for these flowering repressors convert vegetative meristems to flowering branches or flowers. Likewise, in *Arabis alpina* expressing a miR156-resistant version of *SPL15*, most axillary meristems gave rise to flowering branches (Hyun et al. 2019). A similar phenotype was observed when *TFL1* activity was reduced (Wang et al. 2011). *AP2* also acts as a floral repressor in *Arabidopsis* (Yant 2012).

Axillary Meristems that Give Rise to Branches or Flowers

In most angiosperms, axillary meristems on the inflorescence either give rise to branches or flowers. Branches, unlike flowers, usually display internode elongation, produce leaves and secondary branches in addition to flowers and can be indeterminate (*Arabidopsis*) or determinate (pea and rice) (Benlloch et al. 2007). Flowers are determinate, give rise to a finite number of floral organs, and do not generally display internode elongation. In the racemes of *Arabidopsis*, branch fate and indeterminacy of the axillary meristems as well as the primary inflorescence meristem are promoted by *TFL1* (Conti and Bradley 2007), which acts in opposition to factors that induce floral fate, most notably *LEAFY (LFY)* and the *MADS* box transcription factor *APETALA1 (AP1)* (for reviews, see Denay et al. 2017; Wagner 2017). *LFY* is expressed before formation of the first flower in bracts that subtend branches, whereas *AP1* up-regulation occurs later and is restricted to young flower primordia that have committed to floral fate (Alejandra Mandel et al. 1992; Blazquez et al. 1997; Hempel et al. 1997; Yamaguchi et al. 2009). *LFY* directly up-regulates *AP1* (Wagner et al. 1999).

As *AP1* promotes determinacy, branches are formed until *AP1* is up-regulated. The delay in *AP1* relative to *LFY* up-regulation is in part attributable to a requirement for transcriptional cofactors that contribute to *AP1* induction with *LFY* in coherent feedforward loops, such as the *MYB* transcription factor *LATE MERISTEM IDENTITY2 (LMI2)* (Pastore et al. 2011). In addition, gibberellin, which increases during cessation of vegetative development (Galvão et al. 2012; Porri et al. 2012), blocks formation of flowers (Yamaguchi et al. 2014). *LFY* directly up-regulates the *GA*-catabolic enzyme *EUI-LIKE P450 A1 (ELA1)* as well as *GA2* oxidases to enable accumulation of *GA*-sensitive *DELLA* proteins, which complex with the *SBP* transcription factor *SPL9* to activate *AP1* in parallel with *LFY* (Yamaguchi et al. 2009, 2014). Gibberellin also opposes determinacy/flower formation in woody perennial trees such as orange, mango, grapevine, and diploid strawberry (for reviews, see Boss and Thomas 2002; Bangerth 2009; Tenreira et al. 2017). Finally, ubiquitination of *LFY* by *BLADE ON PETIOLE* gene *BOP2* and *CULLIN3 (CUL3)* in seedlings is important for *AP1* induction (Chahtane et al. 2018). This fits with prior findings that *LFY* is posttranslationally activated via ubiquitination and the *F-box* protein *UNUSUAL FLORAL ORGANS (UFO)/CUL1* for flower patterning (Lee et al. 1997; Parcy et al. 1998; Chae et al. 2008). Likewise, in tomato and rice, ubiquitination of *LFY* by *UFO* is required broadly for *LFY* activity (see below).

AP1 is both a direct target of *LFY* and acts in parallel with *LFY* to specify floral fate; this is because of *LFY* independent inputs into *AP1* activation from *FT* and *SPL* transcription factors (for review, see Wagner 2017). Other related *MADS* box proteins, such as *CAULIFLOWER (CAL)* and *FRUITFULL (FUL)* also promote determinacy (Ferrandiz et al. 2000). In addition, consistent with its role in floral commitment, *AP1* directly silences *TFL1* with assistance from the *SEPALLATA* family transcription factor *SEP4* (Ferrandiz et al. 2000; Kaufmann et al. 2010; Liu et al. 2013; Serrano-Mislata et al. 2016; Goslin et al. 2017). Because of its role in the switch to reproductive development (inflores-

cence formation), the role of FT in promoting floral fate is difficult to assess (Yamaguchi et al. 2014). However, FT has been implicated in the maintenance of floral fate during reproductive development (Liu et al. 2014; Müller-Xing et al. 2014).

The above-described factors have largely similar roles in the legumes. In these compound racemes, flowers are not born on the primary inflorescence, which is indeterminate, but on branches (secondary inflorescences), which are determinate. Similar to the scenario in *Arabidopsis*, the pea TFL1 homolog DETERMINATE (DET) and the MtTFL1 of *Medicago* promote indeterminant growth of the primary inflorescence and branch fate in the axillary meristems. Accordingly, the primary inflorescences of *det* or *mttfl1* mutants resemble a flower-bearing branch (secondary inflorescence) and misexpress *VEGETATIVE1* (*VEG1*) and *MtFUL*, respectively (Foucher et al. 2003; Berbel et al. 2012; Cheng et al. 2018). In addition, paradoxically, the uppermost axillary branch meristem of *mttfl1* became indeterminate, phenocopying sympodial growth (Cheng et al. 2018). It would be interesting to explore whether the latter phenotype is caused by competition between MtTFL1 and one of the other three MtTFL paralogs.

Secondary branch fate is promoted by the AGL79/FUL clade MADS box transcription factors *VEG1* and *MtFUL* in pea and *Medicago*, respectively. *VEG1* is expressed in young secondary inflorescences, which are replaced by nonflowering, indeterminate primary inflorescences that express *DET* in *veg1* mutants (Berbel et al. 2012). Similar morphological and molecular phenotypes are observed in mutants of the *VEG1* homolog *MtFUL* in *Medicago* (Cheng et al. 2018). Secondary inflorescence fate is also promoted by pea *VEG2*, a homolog of the bZIP transcription factor FD, which can complex with florigen family proteins (Périlleux et al. 2019). Together with GIGAS/FTa1 (an FT homolog), *VEG2* contributes to secondary inflorescence fate in pea (Berbel et al. 2012; Sussmilch et al. 2015). In addition, *veg2-2* mutants display reduced *VEG1* expression (Sussmilch et al. 2015). Interestingly, in *mttfl1* and *det veg1* double mutants, all secondary inflorescence

branches are replaced by a single flower and the primary inflorescence terminates in a flower (Berbel et al. 2012; Cheng et al. 2018). Thus, DET/MtTFL1 and VEG1/MtFUL not only repress each other (to enable distinct primary and secondary inflorescence development trajectories, respectively), but also jointly prevent floral fate by repressing *PROLIFERATING INFLORESCENCE MERISTEM* (*PIM*)/*MtAPI*.

PIM and *MtAPI* promote floral fate together with the LFY homologs UNIFOLIATA (*UNI*)/SINGLE LEAFLET1 (*SGL1*) in pea and *Medicago*, as well as UFO (Hofer et al. 1997; Taylor et al. 2001, 2002; Cheng et al. 2018). However, compared with *Arabidopsis*, *PIM*/*MtAPI* play a more central role (for review, see Benlloch et al. 2015). *pim* and *mtap1* mutants form *VEG1/MtFUL* expressing I2 inflorescences in lieu of flowers, suggesting that *PIM*/*MtAPI* represses *VEG1/MtFUL* (Berbel et al. 2012; Cheng et al. 2018). As in *Arabidopsis*, only plants mutant for both *MtSGL* and *MtAPI* entirely fail to establish flowers in *Medicago* (Cheng et al. 2018).

Two largely independent regulatory networks control sympodial growth and inflorescence development of tomato. The former centers on TFL1, the second on LFY/UFO as well as additional factors whose *Arabidopsis* homologs have no apparent role in axillary meristem identity. After the transition to the reproductive phase, tomato produces a repeating sympodial unit consisting of three leaves with associated axillary meristem and a terminal cluster of flowers (the inflorescence) (Lifschitz et al. 2014). A specialized axillary meristem associated with the uppermost leaf, the sympodial meristem, repeats this entire unit of development. Mutations in the TFL1 homolog SELF PRUNING (*SP*) reduces the length of the sympodial unit (numbers of leaves produced) and leads to eventual termination in a cluster of flowers. Termination is more extreme in overexpressors of the tomato FT-homolog SINGLE FLOWER TRUSS (*SFT*) and near complete when *SFT* is overexpressed in *sp* mutants, consistent with the idea that the balance between TFL1 and FT homologs determines the switch between indeterminacy/branching and determinacy/flower formation (Lifschitz et al. 2014; Park et

al. 2014; Shalit-Kaneh et al. 2018). An FT homolog that evolved to act as a flowering repressor, SP5G, also contributes to sympodial growth by repressing onset of reproductive development. *sp5g sp* double mutants flower earlier, have shorter sympodial units, and terminate more rapidly in a cluster of flowers (Soyk et al. 2016).

The flower-bearing tomato inflorescence is formed by a sympodial inflorescence meristem, which gives rise to an additional sympodial inflorescence meristem before terminating in a flower; this pattern continues until seven to nine flowers have been formed (Lippman et al. 2008). Branching (formation of sympodial inflorescence meristems) is reduced in the early-flowering *tmf* mutant, which develops a single-flowered primary inflorescence (MacAlister et al. 2012). *TERMINATING FLOWER (TMF)*, which encodes an ALOG transcription factor (MacAlister et al. 2012), likely is not a negative regulator of branching but promotes vegetative identity. The reduced sympodial activity of the *tmf* tomato inflorescence is attributable to precocious activation of *FALSIFLORA (FA)* (*LFY* ortholog) and *ANANTHA (AN)* (*UFO* ortholog). Intriguingly, BOP family members physically interact with TMF and closely related ALOG factors in tomato; the *slbop2* mutant in particular reduces the number of flowers formed per inflorescence (Xu et al. 2016). Complete loss of TMF/BOP activity converts all inflorescences to single flowers (Xu et al. 2016). As outlined above, BOP2 in *Arabidopsis* is required for the ability of LFY to specify floral fate via *API* up-regulation (Chahtane et al. 2018). Thus, different interaction partners with opposite roles in floral fate rely on BOP activity in the inflorescence of *Arabidopsis* and tomato. Whether SIBOP2 posttranslationally modifies TMF is not known.

Consistent with the idea that delayed adoption of floral fate within the inflorescence promotes branch formation, inflorescences mutant for *AN* or *UFO*, *FA* or *LFY*, *COMPOUND INFLORESCENCE (S)* or *WOX9*, are more branched (Lippman et al. 2008; MacAlister et al. 2012). In *an* or *fa* mutants, the primary meristems of the sympodial inflorescence do not form flowers but remain indeterminate, and

repeatedly initiate secondary sympodial inflorescence meristem, which in turn produce more sympodial inflorescence meristems (Lippman et al. 2008). Of note, the tomato and petunia homologs of LFY (*FA* and *ABERRANT LEAF AND FLOWER [ALF]*) are more broadly expressed, but their activity is restricted by *UFO* (*AN* and *DOUBLE TOP [DOT]*), whose accumulation is tightly spatiotemporally controlled (for review, see Moyroud et al. 2010). Inflorescences mutant for *S* fail to properly activate *AN* and initiate additional sympodial inflorescence (Lippman et al. 2008; MacAlister et al. 2012). More recently, elegant genetic analysis implicated three *SEP4* MADS box transcription factors (*J2*, *EJ2*, and *LIN*) in regulating the tomato inflorescence architecture (Soyk et al. 2017). Combination of a weak allele of *j2* with heterozygous *ej2* as well as heterozygous *S* mutants enhanced branching without affecting flower development or fruit set and was thus able to enhance yield (Soyk et al. 2017). The roles and genetic interactions between *WOX9/EVERGREEN (EVG)*, *LFY/ALF*, and *UFO/DOT* are conserved in petunia, which also has sympodial meristems, but forms single flowers (for review, see Castel et al. 2010). As observed in other plant species, the tomato *AP1*-like gene *MACROCALYX (MC)* promotes tomato inflorescence determinacy (Vrebalov et al. 2002; Yuste-Lisbona et al. 2016).

In the grasses, a plethora of distinct inflorescence architectures are found and recent investigations in rice, maize, wheat, barley, and brachypodium are unraveling the genetic basis of each (Bommert and Whipple 2018; Chongloi et al. 2019; Gauley and Boden 2019; Koppolu and Schnurbusch 2019). In the compound inflorescence of rice, flowers are borne on branches, with early arising branches forming secondary branches. Both primary and secondary branches then form spikelet meristems and also terminate in a spikelet meristem. Each spikelet meristem gives rise to a single-flower meristem and flower (Bommert and Whipple 2018; Chongloi et al. 2019). Maize has both male (tassel) and female (ear) inflorescences. The tassel is indeterminate, forming long branches and short branches (spikelet pairs), which in turn gives rise to two spikelet meri-

stems. The ear does not form long branches (Bortiri and Hake 2007; Bommert and Whipple 2018). The spikelet pair and spikelet meristems are considered determinate because of their limited branching capacity (Bortiri and Hake 2007; Bommert and Whipple 2018).

In the rice inflorescence, double mutants in the AP1 and FUL clade MADS box transcription factors *OsMADS14* and *OsMADS15* form an inflorescence and a primary branch meristem but no secondary branches or spikelets (Wu et al. 2017). The phenotypes suggest redundant roles in promoting determinacy, as vegetative structures form in the place of spikelets. The phenotypes and expression patterns of ABERRANT PANICLE ORGANIZATION 1 (APO1/UFO homolog) and APO2/LFY homolog implicate APO1 and APO2 in promotion of indeterminacy; they prevent termination of the primary inflorescence in a spikelet as well as conversion of secondary branches into spikelets (Kyojuka et al. 1998; Rao et al. 2008; Ikeda-Kawakatsu et al. 2012), an apparently opposite function to that of LFY and UFO homologs in inflorescence development of the eudicots discussed above. Similar to rice, maize *zfl2* (LFY homolog) mutants display reduced tassel branching and kernel row number (Bomblies et al. 2003; Bomblies and Doebley 2006). In addition, primary inflorescence meristem phyllotaxis of *apo1* and *apo2* resembled that of the vegetative meristem (Ikeda-Kawakatsu et al. 2009, 2012). Additional studies are needed to understand the role of LFY homologs in monocots and to dissect communalities and differences with eudicot LFY homologs.

Interestingly, although the role of TFL1 family members has thus far mainly been studied by gain-of-function approaches in rice and maize (Nakagawa et al. 2002; Danilevskaya et al. 2010), these studies as well as RNAi knockdown of all rice CENTRORADIALIS (RCN) homologs point to a role of TFL1 in primary inflorescence and branch meristem maintenance, as in the eudicots (Liu et al. 2013). A similar—albeit weaker—phenotype was observed in rice for mutant in *mft1*, one of two MOHTER OF FT AND TFL1 (MFT) proteins of the FT/TFL1/MFT family (Song et al. 2018). *MFT1* overexpression resulted in increased secondary branch formation and

reduced expression of spikelet meristem identity genes, including FRIZZY PANICLE (FZP) (Song et al. 2018), which is discussed in more detail below. Finally, the ALOG transcription factor TAWAWA1 (TAW1), the rice homolog of tomato TMF, prevents premature loss of primary inflorescence activity and conversion of branch meristems into spikelet meristems, at least in part by up-regulating the SHORT VEGETATIVE PHASE (SVP) homologs *OsMADS22* and *OsMADS55* (Yoshida et al. 2013). However, unlike *tmf* mutants, *taw1* mutants are not early flowering. The miR156 targeted SPL family of transcription factors, especially *OsSPL14*, the closest homolog of *Arabidopsis* SPL15 and SPL9, promotes panicle branching, perhaps together with *OsSPL17* (Jiao et al. 2010; Miura et al. 2010; Wang et al. 2015a). Posttranslational modifications also modulate *OsSPL14* accumulation and panicle branching (Wang et al. 2017a,b). Similar roles in inflorescence branching were described for the maize orthologs TASSEL-SHEATH 4 (TSH4), UNBRANCHED 2 (UB2), and UB3 (Chuck et al. 2014).

The AP2/ERF transcription factors BRANCHED SILKLESS1 (BD1) in maize and FZP in rice, as well as their orthologs in barley, wheat, and brachypodium, are markers for and promote spikelet meristem formation (Chuck et al. 2002; Komatsu et al. 2003; Derbyshire and Byrne 2013; Poursarebani et al. 2015). Recently, rice grain number QTLs were mapped to *fzp*, which led to formation of more secondary branches (Bai et al. 2017; Fujishiro et al. 2018). Plants mutant for *Arabidopsis* PUCHI, the BD1 and FZP homolog, have only subtle defects in inflorescence architecture (Karim et al. 2009). Recently, it was shown that FZP down-regulates APO2/LFY in spikelet meristems (Bai et al. 2016). PANICLE PHYTOMER2 (PAP2/*OsMADS34*), a member of a grass-specific clade of SEP proteins, promotes spikelet meristem identity (for review, see Chongloi et al. 2019). Spikelet meristem determinacy, prevention of formation of multiple florets, is under control of microRNA miR172 and its AP2 transcription factor targets INDETERMINATE SPIKELET1 (IDS1) and SISTER OF IDS1 (SID) (Chuck et al. 2007, 2008). IDS1 and SID were first iden-

tified in maize, but have conserved roles in rice, wheat, and barley (Brown and Bregitzer 2011; Lee and An 2012; Lee et al. 2014; Debernardi et al. 2017).

The spikelet pair meristem found in the *Andropogonae*, which includes maize, is considered a determinate branch meristem (Whipple 2017) and gives rise to two spikelet meristems. The genetically defined *RAMOSA* (*RA*) genes promote determinacy in spikelet pair meristems (Bommert and Whipple 2018). *RA1* and *RA2* encode C2H2 Zn-finger proteins and *LATERAL ORGAN BOUNDARY* (*LOB*) transcription factors, respectively (Vollbrecht et al. 2005; Bortiri et al. 2006). *RA3* acts downstream of *RA1* and *RA2* and encodes a trehalose 6 phosphate phosphatase (Satoh-Nagasawa et al. 2006; for review, see Bommert and Whipple 2018). *RA1* is only found in the *Andropogonae* (Bommert and Whipple 2018; Chongloi et al. 2019). *RA1* physically and genetically interacts with a transcriptional corepressor *RAMOSA1 ENHANCER LOCUS2* (*REL*) of the *TOPESS* family, which—as its *Arabidopsis* counterparts—interacts with many transcription factors (Liu et al. 2019b). *rel* single mutants, although pleiotropic, have shorter tassels with reduced branching (Liu et al. 2019b).

CONCLUDING REMARKS

Summary Points

Despite their divergent above-ground architectures, common themes underlie organogenesis, axillary meristem formation, activity, and fate in diverse plant species.

Organogenesis is auxin-mediated and results in initiation of (cryptic) bracts and associated axillary meristems during reproductive development. During vegetative development, axillary meristem initiation is delayed relative to later organ initiation and requires an auxin minimum as well as transcriptional cascades that eventually results in up-regulation of the *STM* pluripotency factor. Axillary meristems arising during vegetative development also frequently remain dormant, and their outgrowth is dependent on interactions between diverse hor-

monal and nutritional cues and a *TCP* transcription factor (Fig. 1).

During reproductive development, meristem activity is strongly influenced by stimuli that promote flowering, with less floral promoting cues leading to vegetative fate in axillary meristems, intermediate floral cues to branching, and strong floral cues to determinacy (see also Prusinkiewicz et al. 2007). With a few exceptions, the functions of key regulators along this spectrum are conserved (Fig. 2). In tomato and rice, *ALOG* family transcription factors control vegetative fate and branching, respectively, whereas additional factors repress excessive branching of the spikelet pair meristem and the spikelet meristems found in maize and rice.

Future Challenges and Link to Crop Yield

Several of the factors described here and their regulatory elements (critical *cis* regulatory elements for transcriptional regulation and microRNA binding sites) were identified as major QTLs for traits linked to yield, highlighting their agronomical importance (Simons et al. 2007; Jiao et al. 2010; Bai et al. 2017; Fujishiro et al. 2018). Genome-wide association studies (GWAS) have also implicated several of the regulators discussed above as important contributors to yield (Olsen and Wendel 2013; Guo et al. 2018). A recent study used GWAS to show that the inflorescence architecture largely determines the efficiency of grain production and yield in wheat (Guo et al. 2018). In addition, genes that contribute to the architecture of the inflorescence, such as *AGL79/VEG1*, *CUC3*, *FZP*, and *TAW1*, are potentially linked to yield enhancement (Crowell et al. 2016; Li et al. 2016; He et al. 2017; Zheng et al. 2017; Fujishiro et al. 2018; Gao et al. 2018; Ta et al. 2018). Studies in other crops, such as maize (Wu et al. 2016), chickpea (Bajaj et al. 2016), and sorghum (Kong et al. 2014), have also dissected the genetic link between inflorescence architecture and yield performance.

Targeted changes in *cis* regulatory elements, by CRISPR/Cas9-mediated *cis* element editing, for example, are emerging as a promising approach. *cis* regulatory mutations that reduce expression of flowering repressor *SP5G* in tomato

	Vegetative	Early reproductive	Reproductive
Organo- genesis	Leaf	Leaf + axillary branch meristem	(cryptic) bract + flower
	Axillary meristem initiation Ls/LAS/MOC1 STM BI/RAX; TAB1; OSH1 DRN, REV	Some effect	
Dormancy/ outgrowth	auxin cytokinin strigolactone sugar TB1/FC1/BRC1 ABA	Some effect	
Identity	mir156* TFL1* PEP1* PEP2*	TFL1 FUL LFY	LFY/BOP2 SEP4 GA AP1
		DET VEG1	UNI PIM
		MtTFL1 MtFUL	SGL MtAP1
		SP SFT	FA/AN J2, EJ2 MC
	OsMADS14/RCN APO2/APO1 OsMADS14 ZFL	PAP2/OsMADS34	
	Branches/tillers	Primary and secondary branches	Flowers

Figure 2. Key regulators of plant inflorescence architecture and their function are conserved in diverse flowering plants. Regulators are grouped based on the developmental phase they act in (boxes) and from less (*left*) to more (*right*) determinate in each phase. Homologs in different species are color coded. *Vegetative axillary meristem identity was only discussed for *Arabidopsis* and *Arabis alpina* (see text for additional details).



led to loss of day length sensitivity and—combined with mutations in *sp*—to a higher harvest index in field conditions (Rodríguez-Leal et al. 2017; Soyk et al. 2017). Regulatory changes may also avoid negative epistasis by lowering rather than blocking gene function of multiple loci to “improve” inflorescence architecture. This was shown by stacking of weak alleles that minimize detrimental effects on other traits like fruit development and enhanced yield of a cherry tomato variety in greenhouse conditions (Soyk et al. 2017). That CRISPR/Cas9 approaches that target domestication genes can lead to rapid increase in fruit size and number in wild relatives was also recently shown in tomato (Zsögön et al. 2018). In addition, microRNA-resistant alleles of the *OsSPL14/IPA1* transcription factor in rice enhance panicle branching and increase yield in field conditions (Jiao et al. 2010; Miura et al. 2010) as well as disease resistance (Liu et al. 2019a).

All of these approaches will profit from increased understanding of the key players and their regulatory interactions. For example, iden-

tification of direct targets of transcriptional regulators by chromatin immunoprecipitation and defining the underlying *cis* motifs will allow precise “rewiring” of specific regulatory interactions by CRISPR/Cas9 mutagenesis of noncoding DNA. As many regulators have multiple roles in diverse aspects of inflorescence development, more precise insight into their role in a given process/trait of interest, for example by cell-type-specific loss-of-function mutants, is important. These types of analyses are facilitated by development of new technologies, such as targeting of dCas9 fusions with strong transcriptional repressor domains (Lowder et al. 2015; Piatek et al. 2015).

Similarly, because several of the regulators discussed here act cell nonautonomously (for review, see Bommert and Whipple 2018) or are mobile (TFL1, FT, LFY, STM) (Lucas et al. 1995; Sessions et al. 2000; Conti and Bradley 2007; Jaeger and Wigge 2007), it will be critical to identify their precise sites (cell type) of activity, for example by confocal imaging of the localization of the relevant proteins. Recent advances in gene

targeting in plants might be especially helpful to achieve this goal (Miki et al. 2018; Huang and Puchta 2019). The real payoff, for mechanistic insight into plant architecture and for crop improvement alike, is that these approaches—when applied to plant species with diverse inflorescence architectures—will reveal commonalities and differences in the regulatory components and their interactions and hence the “wiring plan” that gives rise to distinct inflorescence architectures.

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