Shoot meristems of deciduous woody perennials: self-organization and morphogenetic transitions
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Shoot apical meristems of deciduous woody perennials share gross structural features with other angiosperms, but are unique in the seasonal regulation of vegetative and floral meristems. Supporting longevity, flowering is postponed to the adult phase, and restricted to some axillary meristems. In cold climates, photoperiodic timing mechanisms and chilling are recruited to schedule end-of-season growth arrest, dormancy cycling and flowering. We review recently uncovered generic meristem properties, perennial meristem fate, and the role of CENL1, FT1 and FT2 in bud formation and flowering. We also highlight novel findings, suggesting that dormancy release is mediated by mobile lipid bodies that deliver enzymes to plasmodesmata to recover symplasmic communication and meristem function.

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Introduction
The generic structural and geometric properties of the angiosperm shoot apical meristem (SAM) reflect the overall organization of the underlying signal networks that drive meristem function, even though specific genes may differ [1]. These networks give rise to a proliferating context that reciprocally feeds back on them, channeling and restraining signal distribution, and diversifying gene expression and cell proliferation [2,3]. For descriptive reasons, classic models highlighted structural features of the angiosperm SAM, depicting its organization as ‘duplex’. Duplex thereby refers to the presence of two superimposed developmental zones, a curved sheet (tunica) and a subjacent corpus, that are derived from stacked sets of stem cells [3,4]. Cyto-histologically, the SAM was described in terms of a central and peripheral zone with distinct cellular activities [3,4]. Although these models remain valuable as descriptive contexts, from a system dynamics perspective the SAM might best be understood and modeled as a self-organizing system. We here describe some processes that contribute to SAM integration and highlight the added value of studying the SAM of deciduous woody perennials. The deciduous life-style originated in the tropics as an adaptive response to drought, pre-adapting perennials to life in cooler regions with longer photoperiods [5]. In temperate and cold regions the deciduous and periodic growth habit evolved into a unique trait by recruitment of photoperiod-based timing mechanisms that schedule growth cessation and arrest of meristems in dormant winter buds. As these traits are unique to perennials, their investigation might uncover meristem properties that are missing or less amenable to scientific investigation in annuals.

Mechanical frameworks and PD connections
The tunica and corpus represent very different growth zones. In the tunica, cells proliferate in two dimensions, creating an expanding sheet, whereas in the corpus growth is three-dimensional. This condition gives rise to complex physical interactions. Recent investigations using atomic force microscopy to measure compressibility of the SAM showed that the surface of the central zone is relatively stiff while the peripheral area is more moldable, matching their contrasting patterns of slow isotropic and accelerated anisotropic growth, respectively [6**,7]. This is paralleled by the distribution of cortical microtubules (CMT), which are oriented randomly in the central zone but force-aligned in the peripheral zone [8,9**]. Such investigations emphasize the notion that morphogenesis at the SAM is guided by physical forces, sustained by feedback from gene expression and cell wall metabolism [6**,7,9**,10**,11].

Additionally, the duplex nature of the angiosperm SAM dictates its symplasmic organization. A symplasmic map shows that tunica and corpus are symplasmically subdivided into sectors that represent branched lineage trees that spring off from the centrally located stem cells or ‘initial’ cells [3]. Adjacent lineage branches and sectors (lineage trees) are secondarily interconnected via PD that are produced de novo in existing cell walls. The resulting symplasmic network is indispensable for
cell-cell signaling in the SAM, and to ensure the symplastic unity of the emerging shoot system. Indeed, in many lower vascular plants that are unable to produce secondary PD, the shoot system represents a single complex cell lineage which is produced from a single top cell [3]. It is becoming increasingly clear that the symplastic organization [2,3] has an important role in the 'developmental programming' [4] of the SAM. Woody deciduous perennials dissipate this symplastic organization in a developmentally controlled manner as part of an adaptive trait to arrest growth before the arrival of winter, and re-establish it in anticipation of growth renewal in spring [2,12].

Symplasmic fields
Despite the fact that all cells are interconnected by PD, the duplex SAM is not a single symplasmic continuum. On the contrary, it is dynamically partitioned into symplasmic fields (SFs) by the positional closing of PD between the central and peripheral zone [2,3,12–14]. While the mechanism that keeps PD in check at these strategic positions has not been identified, recent investigations on SAM compressibility and elasticity may provide some clues [6**,7,8,10**]. The centrally located SF (CSF) [2,12–14] corresponds to the domain of isotropic growth in the central zone of the tunica, while the peripheral SF (PSF) corresponds to the anisotropically growing peripheral zone. The two distinct growth domains also differ in elastic properties, that is, in their capacity to yield to turgor stress [10**]. The symplasmic border between the CSF and the PSF may coincide with the boundary region between the two elastic domains, suggesting that PD closure relates to an abrupt change in elasticity. If so, the mechanism of such PD closing would need to be established. It is tempting to speculate that the isotropic growth in the central domain, resulting from random distribution of CMTs throughout this domain [6*,7], is due to the cytoplasmic union of the cells in the CSF as it provides metabolic and electrical coupling [2,15]. Similarly, anisotropic growth could underlie the interruption of the PSF at putative positions of incipient primordia [2]. Recently, two members of a family of PD-located protein1 (PDLP1) that modulate PD permeability were found to be differentially expressed in the SAM in areas that closely correspond to the CSF and PSF [16]. This is the first evidence that PD regulation differs between SFs.

The CSF and the PSF are integrated into the overall symplasmic organization of the SAM by exchange of morphogens and transcription factors via gating PD [17–20,21*], and by ligand–receptor interactions that bridge the extracellular space [22]. Another layer of regulation is provided by the differential gating of primary and secondary PD [3]. In support of this, some mobile transcription factors move selectively and directionally within the SAM [18,19,21*]. Mobile microRNAs may also cross SF boundaries through gated PD, contributing to SAM stability [23]. Collectively, these complimentary forms of communication support a model that depicts the SAM as a morphogenetic unit that is characterized by extensive feedback and self-regulation [24]. Despite its semi-autonomous organization, the SAM is highly sensitive to specific inputs from the shoot and the environment, to which it can respond with morphogenetic transitions [2,12–14,25–27].

SAI transitions
Perennials undergo specific transitions during their life cycle, triggered by external and endogenous signals (Figure 1). The juvenile phase is extended over multiple years and, as in annuals [28], the transition to the adult stage is regulated by microRNAs [29]. Flowering occurs only in the adult phase [30,31] and is restricted to a subset of axillary meristems (AXMs) to ensure continuation of vegetative growth [32,33,34**]. Another trait vital to survival is the capacity of meristems to transit into a dormant and freezing-tolerant state at the end of the growing season [12,27,35]. The biology of these seasonal transitions in SAM behavior cannot be investigated in Arabidopsis, perhaps explaining why the understanding of their molecular regulation is still limited. Fortunately, this is now changing as a number of tree genomes has been sequenced, among which is the Populus trichocarpa genome [36]. Thus far, investigations have focused on identifying input signals from the leaves that lead to transitions at the apex.

The leaf-generated signal FLOWERING LOCUS T (FT) is central to flowering in Arabidopsis and other perennials, including poplar [14,27,30,37], citrus [38] and apple [39]. FT peptides are produced in the leaves and must be transported to the apex to evoke floral transitions. An influential study in hybrid aspen showed that long days (LD) positively regulate the CONSTANS/FT module to induce flowering in adult trees [27]. In addition, short days (SD) rapidly downregulate FT, resulting in growth cessation, bud set, and dormancy [27]. Similar effects have been documented for plum [40]. In adult Populus deltoides trees, one of the FT paralogs, F2, was reported to regulate flowering [30], but subsequently it was concluded that this might not be its major function [34**]. Vegetatively growing juvenile hybrid poplar expresses F2, but under SD it is rapidly downregulated before growth cessation and formation of dormant buds [14]. During chilling-induced release from dormancy, the paralog FT1 was hyperinduced in the bud [41**]. A year-round transcript profiling study of adult field-grown trees confirmed that FT1 and F2, although very similar [30], may deviate in regulation and function [34**]. F2 is expressed during growth in the leaves and downregulated by SD, whereas its transgenic overexpression prevented growth cessation and bud set [34**]. In a similar fashion, F2 remains highly expressed under SD in PHYA over-expressing hybrid poplar that failed to set bud and enter

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Environmental effects on meristem function. (Left panel) Plants respond to environmental changes, which are registered via sensory systems in specialized tissues and cells. Perceptions are translated into long-distance endogenous signals that are transmitted to growth moldable centers, among which the shoot apex. (Middle) The perception of a critical photoperiod in the leaves may differentially affect the two meristematic areas in the apex, RM and SAM, so that their activities potentially can be uncoupled. During vegetative growth and development the SAM and the RM carry out specific activities (listed within the circle). (Right panel) The SAM is involved in the cyclic activity of phyllotactic patterning (A), and may respond to environmental conditions with a transition to an inflorescence or floral meristem (B), or entry into the dormancy cycle (C). The RM has only two choices, activity (arrow) or inactivity (bars). Long-distance signals like FT first arrive at the RM (+ positive signals, – negative signals), which may be regarded as a relay-station that modulates and distributes signals. Phyllotaxis (A) and flowering (B) may proceed with or without RM activity, while dormancy (C) requires an inactive RM. SAM transitions between A and C (arrows) occur during perennial juvenility and in a subset of buds in adult perennials, that is, in non-flowering vegetative buds (double bars in C). The transition to flowering represents end-differentiation (bar in B).

dormancy [14]. Thus, it may be concluded that in juvenile trees [14,41**] as well as in adult trees [34**] FT2 is expressed during vegetative growth in leaves, whereas FT1 is recruited by chilling in dormant buds [34**,41**] to prepare for vegetative growth in spring as well as floral transition in susceptible AXMs. There might then be four different FT1-expressing dormant buds: terminal buds, and AXBs that either will grow vegetatively or fl Orr that in the new growing season, or remain quiescent. In the latter, FT1 might be inhibited by a homolog of the

*Arabidopsis* protein BRANCHED1, which effectively neutralizes FT (and TSF) by binding to it without involvement of 14-3-3 proteins [42**]. While in perennials FT1 and FT2 may function annually in different seasons, in the biennial plant sugar beet they function in the juvenile and adult stages during two successive years [43**]. The evolutionary significance of such gene duplication is that it may serve diversification of gene function and the emergence of new adaptive traits, for example involving downstream targets, or regulatory loops that
control seasonal and tissue-specific expression. Even genes that regulate FT expression in Arabidopsis, such as CO, might not be widely conserved [44], considering that overexpression of two poplar homologs, CO1 and CO2, did not affect flowering, growth cessation and bud set in poplar [45].

**The putative relay function of the RM**

FT is presumably loaded into the sieve tubes, possibly with the assistance of FT-INTERACTINGPROTEIN 1 [46], for transport toward the apex where it arrives at the rib meristem (RM), a domain just below the SAM [47] (Figure 2a-d). The RM is a genuine meristem which regulates stem elongation in caulose plants, and inflorescence elongation in rosette plants [47-50]. It is significant that RM activation in rosette plants is integral to the flowering process and that, reversely, a rossette-like growth habit can be experimentally induced in caulose plants [48,51] (Figure 2e-g), and temporarily even in poplar [14]. Once FT arrives at the RM [47], the meristem-identity gene TERMINAL FLOWER1 (TFL1) [52] is upregulated as a consequence [53]. From there, the TFL1 protein traffics to the SAM through PD to safeguard the indeterminacy of the SAM [53] which might involve competition with FT for binding to the bZIP factor PD in a complex with a 14-3-3 receptor protein [53-55]. In contrast, FT2 production in the leaves of SD-exposed poplar ceases while the TFL1 ortholog CENTRAL RADIUS LIKE1 (CENL1) is transiently upregulated in the RM zone [14], leaving CENL1 without competitor. It seems possible that CENL1, in a similar manner as TFL1 in Arabidopsis, binds to its interactors, safeguarding SAM indeterminacy during dormancy and subsequent quiescence. Transgenic studies show that overexpression of FT and CENL1 interferes with dormancy regulation (Figure 2h-k), underlining the importance of these genes for the proper regulation of RM and SAM behavior. It seems possible that the RM functions as a signal hub and integrator of the input signals that are destined for the SAM (Figure 1). This interaction between the RM and the SAM may be key to understanding various developmental phenomena specific to perennial apices, including the distinction between short and long shoots, rosette and caulose growth, as well as bud formation [49,50].

**The transition to dormancy**

The SD-induced downregulation of FT2 in leaves is a key event as it is followed by a shift from leaf to scale production, the first sign of terminal bud formation (Figure 3). However, the downregulation of FT2 is not the direct cause of dormancy as growth can resume when juvenile trees are returned to LD for at least for 2 weeks after FT2 downregulation [14]. Moreover, the SAM remains morphogenetically active for some time in order to produce a miniaturized shoot, referred to as an embryonic shoot (ES), inside the bud [49]. The terminal bud with its enclosed ES survives through winter, and serves to kick-start growth in spring. Thus, considering that FT2 downregulation halts RM activity and promotes scale leaf production, FT2 protein might be required to drive RM function during vegetative growth. Remarkably, an ES similar to the one in SD-induced terminal buds is also produced under LDs in quiescent AXBs. As terminal buds upregulate CENL1, which is characteristic of AXBs [33], the SAM apparently adopts the developmental program of the AXBs before dormancy establishment. Despite these similarities, the initiating factors as well as those that keep the terminal buds and AXBs inactive are different. As AXBs develop under LD by default, FT2 downregulation is not the triggering factor, as in case of terminal buds. Once formed the non-dormant AXBs are kept quiescent by subtending leaves [50] and apical dominance [56].

Gene expression profiling has pinpointed a number of relevant genes in developing terminal buds, but understanding their precise function is challenging because many different tissues develop alongside each other. For example, after 2–3 weeks of SD, AINTEGUMENTALEIKE1 (AIL1) [57] and GA-INSSENSITIVE (GAI) [35] are downregulated. Loss of AIL1 blocks cell divisions, presumably in embryonic leaves as RM and SAM cease cell division activity before this point in time. Most gene expression changes in poplar are found at SD weeks 3 and 4, and relate to cell cycling and acclimation [35]. At this point several hormone signaling genes are upregulated, including those involved in the biosynthesis of ethylene and abscisic acid (ABA) [35]. Dormancy-associated MADS-box genes (DAM) are also implicated as their expression correlates with the dormancy induction period [58,59,60,61*]. Genes that regulate GA biosynthesis and signaling, and genes that regulate production of callose-degrading GH17 family proteins (1,3-β-glucanases) are differentially regulated throughout the SD-induced trajectory [41**]. The downregulation of growth-related GH17 genes commences directly after SD perception, and in connection to the downregulation of FT2 in the leaves. As a consequence of this, possibly together with an increased 1,3-β-glucansynthase activity, all sympatric pathways in the SAM become obstructed by callose (1,3-β-glucan) depositions in dormancy sphincter complexes (DSC) at PD (Figure 2a, b). DSCs function as circuit breakers in the sympatric circuitry of the SAM, preventing electrical and metabolic coupling as well as the exchange of transcription factors. As a result SAM functioning is arrested [2,12,14,24].

**The release from dormancy**

In order to resume growth, the dormant SAM needs adequate exposure to chilling, followed by a rise in temperature (Figure 3). Gibberellic acid (GA) application can replace chilling, albeit reported results have been somewhat ambiguous. This is probably due to application
Structural and functional properties of meristems. (a–d) Generic aspects. (a) The poplar apex, as all angiosperm apices, has a duplex organization composed of a tunica and corpus, and a superimposed central zone (CZ) and peripheral zone (PZ). (b) Detail of a boxed area in (a) showing a rib meristem (RM), located immediately subjacent to the shoot apical meristem (SAM) and characterized by cell plates that become oriented in the
of different GA forms, as apparent from recent research that uncovered key molecular mechanisms behind these responses [41**]. A commonality for both chilling and GA-treatment is that both facilitate the removal of callose depositions at PD-DSC and phloem through recruitment of GH17 enzymes (1,3-β-glucanases), thereby restoring PD conductivity, and allowing the reconstitution of the symplasmic organization of the SAM. In case of chilling-induced release from dormancy, lipid bodies (LB) may play an important role [12] (Figure 2l, o–q). During bud formation, and coincident with the upregulation of ethylene signaling genes [35], numerous LBs are pinched off from the ER [41**,62], where also the ethylene receptor is localized [63]. Although originally viewed as simple lipid storages, LBs have recently emerged as genuine organelles that can act as mobile platforms on which signal molecules and enzymes take a ride to various destinations in the cell [62,64**]. Results from transient expression and co-localization studies of GH17 enzymes support the role of a LB-based delivery mechanism to the PD. This led to the identification of distinct types of GH17 proteins that function in the dormancy cycle, including those which possess a CBM43 carbohydrate binding module [65], a GPI-anchor [65], and homology to a birch LB-GH17 protein [41**]. These enzyme classes are differentially regulated by SD, chilling, and GA$_3$ and GA$_4$ application. Significantly, GA$_3$-application promoted expression of LB-GH17 enzymes, while GA$_4$ promoted those with a GPI-anchor. Moreover, LB-GH17s were induced under SD while GPI-anchored GH17s were downregulated, suggesting that a shift in GA biosynthesis occurred under SD. Although the different types of GH17 proteins were equally able to target PD, they are likely to be delivered by distinct mechanisms, and to different PD sites. GPI-anchored GH17 proteins are presumably delivered via the Golgi excretion pathway to the extracellular leaflet of the plasma membrane, where they attach their GPI anchor. Subsequently, they might move laterally to the PD exterior to hydrolyze the extracellular callose ring of the DSCs [41**,62]. In contrast, LB-associated GH17s may reach PD via fusion with the cytoplasmic leaflet of the plasma membrane [41**]. In the light of the finding that membrane rafts may shuttle proteins like remorin to the PD cavity [66], it seems plausible that the recruitment of GH17 enzymes to the PD neck and channel involves rafts.

**Epigenetic regulation of dormancy**

Dormancy release and vernalization have often been suspected to be very similar processes [67]. Both require low temperature for an extended period to proceed, both are quantitatively in nature, and in both cases the site of perception is the SAM [12,68]. In vernalization, one of the best characterized epigenetic processes in plants, chilling stably represses the central floral inhibitor FLOWERING LOCUS C (FLC), a MADS box transcription factor [69]. Recent advances include the involvement of the intriguing newcomer ‘long noncoding RNA’ (lncRNA) [70,71]. Although little is known about epigenetic mechanisms in woody perennials, it is likely that crucial differences exist. For example, the epigenetic patterns established during vernalization are mitotically stable and transmitted to daughter cells where FLC silencing is maintained even after return of warm conditions [69]. In contrast to vernalization, chilling-induced release from dormancy and acquisition of freezing-tolerance are not retained when temperature rises, as the SAM rapidly deacclimates. Nevertheless, histone modifications and DNA methylation might take place during various phases of the dormancy cycle. After 1 week of SD, poplar apices strongly upregulate four genes involved in chromatin remodeling (CDC48-like, Histone 1-3, FERTILIZATION INDEPENDENT ENDOSPERM, and PICKLE) [35]. Investigations in chestnut showed that genomic DNA methylation increased during bud set and decreased during bud burst, while H4 acetylation, associated with transcriptional activation, showed the opposite [72]. DAM1 gene in leafy spurge is regulated in the bud at least in part by histone modifications, as apparent from altered levels of H3K4me3 and H3K27me3 during the transition from dormancy to a quiescent state [58]. In peach, the DAM6 gene similarly becomes enriched with

(Figure 2 Legend Continued) horizontal plane to give rise to the cell files of the rib zone (RZ) and pith (a and b; from [14]). Inset in (b) shows unmodified plasmodesmata during growth (from [12]). (c) Microinjection of Lucifer Yellow shows that the cells in the central zone of the tunica of birch, as well as in other angiosperms, are symplasmically coupled into a symplasmic field that is shielded off from the peripheral cells by positional closing of plasmodesmata (from [23]). (d) The rib meristem in poplar, as in other angiosperms, may be relatively separated from the SAM by the narrowing or closing of plasmodesmata, as shown by Lucifer Yellow microinjection (from [14]). (e–k) Meristem transitions. (e–g) The caulescent plant tobacco can be forced to grow as a rosette (e) by arrest of rib meristem activity (f) through overexpression of viral protein that targets plasmodesmata, while SAM activity continues like in wild type (g); T; tunica; C; corpus; RM; rib meristem; RZ; rib zone (from [51]). (h) Under short days the perennial SAM develops a terminal bud, while PHYA overexpressors (inset) fail to set buds or assume dormancy (from [14]). (i) Overexpression of FT prevents bud formation (inset) while wild type plants assume dormancy (from [27]). (j) Overexpression of poplar CEN delays bud flushing (from [33]). (k) In contrast to wild type plums, which assume dormancy, FT overexpressors show continuous flowering and fruit set, flowers; if, immature fruits; r, ripening fruits (from [40]). (l–n) PD modifications. (l) During short day-induced bud set numerous lipid bodies (arrows point at examples in L1 and RM; detail in inset) are produced in the SAM and RM (from [62]), while plasmodesmata are closed by callose (black deposits) (m; from [41**]) that is deposited in dormancy sphincter complexes in the cell wall (cw; arrow) and the plasmodesmal channel (PD; arrowhead) (n; from [12]). (o) Chilling displaces lipid bodies (LB) to the cell wall (cw) and plasmodesmata (arrowheads), where callose is hydrolyzed (from [12]), whereas without chilling this does not happen (p; from [41**]). Application of GA$_4$ results in callose disappearance at plasmodesmata (PD; arrowheads) without lipid body (LB) movement to the cell wall (cw) (q; from [41**]). (r) Callose, as shown in (n), is present as a mixture with tannic acid stained proteins in the plasmodesmal channel (PD; arrow head) and the external PD ring (arrow) in the cell wall (cw) (from [12]).
H3K27me3 during dormancy release [73]. A recent study in poplar showed that, DNA methylation was extensive and variable among different tissues. In addition, gene body methylation was transcriptionally repressive, in contrast to Arabidopsis where body methylated genes are often transcriptionally active [74]. In the cells of the poplar SAM DNA methylation mapped in the open chromatin fraction is widespread and variable among the genes [75]. Further investigations on epigenetic regulation of genes involved in dormancy cycling (Figure 3), are expected to contribute new insights into the nature of this seasonal transition in perennials.

**Conclusions and perspectives**
Recent studies bring into focus the notion that the SAM is a highly dynamic and integrated system with feedback at various levels that sustains its organization and functioning. Furthermore, the RM emerges as a putative signal integration and relay station [14,47,53,54], complementing its role in stem elongation [48–51]. Uniquely, perennial shoot meristems proliferate only for a restricted period of time in each growing season, while substantial time is invested in preparing for the establishment and release of dormancy, flowering, and growth resumption. In these processes, the paralogs FT1 and FT2 [34**,41**] underlie some of the
novel adaptive traits that arose through genome duplication and recruitment by different regulatory loops. Similarly, the members of the GH17 family are recruited by different seasonal processes [41**] suggesting that members of other gene families with seasonally diversified regulation and function are awaiting discovery. Specific GH17 enzymes are delivered to the PD, possibly in conjunction with a host of other proteins. The fact that L Bs amass in apices of perennials during bud formation makes this unique proteome amenable to analysis. In addition, it will be opportune to assess how stem cell identity and meristem organization are maintained during the long periods of inactivity, dormancy and quiescence. In the near future, research endeavors on perennial shoot apices are expected to enrich our knowledge and broaden the concept of these intricate entities we call meristems.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

● of special interest
■ of outstanding interest


This study used atomic force microscopy to investigate the compressibility of SAM cells in relation to morphogenesis at the SAM. The authors show that the mechanics of the extracellular matrix plays a role in the shaping of the SAM. They established that the central region of the SAM surface is considerably stiffer than the peripheral zone where primordia are initiated. With a transgenic approach it was shown that this required a decrease in pectin methylation.


The authors addressed the role microtubules play in the mechanical modulation of morphogenesis at the SAM. They made use of mutants that were impaired in the protein katanin, which functions to severe microtubules. As a result microtubule dynamics was disturbed resulting in the incapacity of cells to respond to mechanical forces. The SAM of the mutant showed a crater-like depression, which was ascribed to increased anisotropy in the peripheral zone, suggesting that growth rate and growth anisotropy need to be tightly regulated to maintain a dome-shaped SAM.

10. Kierzkowski D, Nakayama N, Routier-Kierzkowska A-L, Weber A, Bayer E, Schor better M, Reinhardt D, Kuhlemeyer C, Smith RS: Elastic domains regulate growth and organogenesis in the shoot apical meristem. Science 2012, 335:1096-1099. This important study explores the mechanical properties of SAM cells in terms of their elasticity, instead of their compressibility. The results indicate that the local yielding of the peripheral SAM surface during primordia formation (bulging) is related to the relaxation of the cells when under hydrostatic pressure. The authors established that the central zone displays considerable strain stiffening, and they propose that differences in strain stiffening contribute to the zonation of the SAM.


The authors demonstrate with a series of ingenious experiments that a number of MADS domain proteins traffic through plasmodesmata in the inflorescence and floral meristem of Arabidopsis, but that there was a difference in their ability to move through secondary plasmodesmata that interconnect the tunica and corpus.


This paper provides a mechanistic explanation for dormancy release by chilling and gibberellic acid (GA). GH17 proteins (1,3-β-glucanases) localized to PD and were differentially regulated by long day, short day and chilling, as well as by GA4 and GA25. Chilling is shown to hyperinduce FT1 in the dormant bud, whereas CEN/FT/L1 requires a subsequent temperature rise. A heuristic model puts the data in context.


The authors identified BRC1 as an interactor of FT. Binding results in a delay of floral transition in axillary meristems. It is shown that interaction does not involve 14-3-3 proteins, like in case of TFL1, which modifies FT function through FD.


Evidence is presented that in the biannual sugar beet the paralogs FT1 and FT2 have diversified to function in the juvenile and adult phases, respectively, in its two growth seasons.


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The authors identified 23 genes that were upregulated during short day exposure in wild type as compared to the evergreen mutant (evg) which is unable to assume dormancy. Of special interest are two DAM genes, DAM1 and DAM6 which expression is continually increasing and might intimately be connected to establishment of dormancy.


64. Murphy DJ: The dynamic roles on intracellular lipid droplets: from archaea to mammals. Protoplasma 2012, 249:541-585. The author provides an extensive overview of the historic as well as emerging role of lipid droplets (lipid bodies), and highlights their dual role as storage for lipids and novel plant organelles with multiple functions in organelar interaction, defence and signalling.


The authors demonstrate that the ‘methylated DNase I hypersensitive chromatin fraction’ in the poplar SAM covers 1.9% of the genome (representing 74% of poplar v2.0 gene models). They find a higher percentage of promoter (26%) and body-methylated (55%) genes in comparison to other studies using a whole-genome approach.

Description box

Dormancy: A state of self-arrest of the SAM which is maintained under growth-promoting conditions.

Dormancy Sphincter Complexes: Circuit breakers in the symplasmic circuitry of the SAM which are installed at plasmodesmata during dormancy establishment.

Embryonic Shoot: The dwarfed and incompletely developed shoot produced by an axillary meristem or SAM inside an axillary and terminal bud, respectively.

Symplasmic Fields: Positionally determined symplasmic compartments in the proliferating SAM. SFs are morphogenetic fields that unite cells cytoplasmically, allowing metabolic and electrical coupling as well as direct exchange of morphogens. They correspond to central/ peripheral SAM zones, and to a central stiff area of isotropic growth and a more mouldable anisotropic growth area where leaf buttresses arise.

Plasmodesmal Gating: The regulated transient opening or widening of plasmodesmata that allows passage of transcription factors and signaling molecules by simple diffusion or targeted transport.

Quiescence: A resting state sensu lato: (1) A para-dormant state of an axial bud, imposed by the shoot system under conditions that promote growth. (2) An eco-dormant state of terminal and axillary buds, imposed by suboptimal environmental conditions. Quiescence can be released by removing the sources of suppression.

Rib Meristem: A derived meristem immediately subjacent to the SAM corpus where cell division plates are aligned in the horizontal plane, giving rise to the cell files/ribs of the rib zone.

Symplasmic Map: Diagram depicting the location of primary (cell plate) plasmodesmata and secondary (inter-lineage) plasmodesmata.