


# When to branch: seasonal control of shoot architecture in trees

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Long-lived perennial plants optimize their shoot architecture by responding to seasonal cues. The main strategy used by plants of temperate and boreal regions with respect to surviving the extremely unfavourable conditions of winter comprises the protection of their apical and lateral meristematic tissues. This involves myriads of transcriptional, translational and metabolic changes in the plants because shoot architecture is controlled by multiple pathways that regulate processes such as bud formation and flowering, small RNAs, environmental factors (especially light quality, photoperiod and temperature), hormones, and sugars. Recent studies have begun to reveal how these pathways are recruited for the seasonal adaptation and regulation of shoot architecture in perennial plants, including the role of a regulatory module consisting of antagonistic players terminal flower 1 (TFL1) and like-ap1 (LAP1) in the hybrid aspen. Here, we review recent progress in our understanding of the genetic control of shoot architecture in perennials compared to in annuals.

## Introduction

Environmental factors such as light and temperature play crucial roles in the regulation of plant growth and development. Both of these factors constantly change throughout the day and seasonally throughout the year. In temperate and boreal regions, these

changes can be very extreme. In summer, days are long and temperatures are moderate, favouring plant growth and development, whereas, in winter, days are shorter and temperatures are lower, restricting active growth. Thus, perennial plants in these regions must

## Abbreviations

ABA, abscisic acid; AIL1, aintegumentalike 1; BRC1, branched 1; CENL1/TFL1, centroradialislike1/terminal flower 1; CK, cytokinin; CO, constans; EBB1, early bud-break 1; FT, flowering locus T; GA, gibberellin; LAP1, like-AP1; MAX1, more axillary branches 1; phyB, phytochrome B; PIF8, phytochrome interacting factor 8; RAV1, related to ABI3 and viviparous 1; SL, strigolactone; TEM1, tempranillo 1; VvBRC1, *Vitis vinifera* BRC1.

cyclically protect their sensitive meristematic tissues that are responsible for growth in the unfavourable conditions prevailing in winter through dormancy and then restart active growth when favourable conditions return in spring [1,2]. However, other than external environmental factors, various internal factors (such as hormones, sugars and other metabolites) also participate in the control of plant growth [1,3], and so both environmental and internal factors control and tune the seasonal growth and dormancy in perennial plants.

Key architectural features of perennial plants, particularly trees and shrubs, include the terminal (or apical) buds and the axillary (or lateral) buds located at leaf axils, which enclose the axillary meristems responsible for branch formation. Substantial information on the seasonal cues and controls of apical meristem growth and its cessation is available [4–8]. By contrast, how seasonal cues regulate the growth and development of axillary meristems remains poorly understood, despite the apparent importance of the tight regulation of axillary bud development, dormancy and outgrowth for plant survival, growth and architecture. The fate of an axillary bud to outgrow or remain dormant is also developmentally and seasonally regulated.

Shoot branching has been mainly investigated in annual plants, especially *Arabidopsis* and pea, and several putative regulatory mechanisms have been proposed for this process [9,10]. These plants present several advantages for their investigation, including a short life cycle, available genome sequences, well-understood genetic properties and a convenient size [11–13]. However, they cannot provide information on key aspects of perenniality, and so, in recent years, studies have been extended to many perennial model systems, such as *Arabidopsis*, rose, apple, grapevine, peach, and several species and hybrids of *Populus* (hereafter poplars) [14–21]. In many of the plants noted above, studies of shoot branching regulation have focused on the effects of apical dominance on branching, largely in classical decapitation experiments, rather than effects of seasonal regulation, and so the key questions remain unanswered. Few studies have been carried out previously on *A. alpina*, a perennial relative of *Arabidopsis*, with the aim of exploring the annual to perennial transition and the involvement of seasonal factors [22,23]. In this review, we discuss our understanding of shoot branching, the mechanisms involved and its regulation by seasonal factors, especially photoperiod and temperature, in perennials. Also, how similar and different are various models in perspective of temperate trees.

## Seasonal control of branching in perennial plants

Genetic, molecular and biochemical studies involving many branching-related genes and hormones, such as branched 1 (BRC1), auxins, strigolactones (SLs), cytokinins (CKs) and gibberellins (GAs), in annual and perennial plants suggest a very high level of functional conservation in branch development in evolutionary transitions from annuality to perenniality, and vice versa [9,10,15,16,19,24,25]. However, environmental factors, mainly light and temperature, play additional roles in seasonal regulation in perennials. For example, vernalization or low-temperature treatment induces flowering in *Arabidopsis* and *A. alpina*, whereas, in the latter, it also enhances dormancy of axillary buds, and hence participates in the seasonal control of its branching [21]. Further clues about the seasonal regulation of axillary bud outgrowth have been obtained from overexpression of *Castanea sativa* related to ABI3 and viviparous 1 (RAV1), a homologue of *Arabidopsis* tempranillo 1 (TEM1), in poplar. The transgenic poplar line overexpressing *RAV1* develops early branches in the same seasons compared to control wild-type plants. *CsRAV1* mRNA expression shows a robust circadian rhythm pattern, peaking at noon in chestnut plantlets grown under long-day conditions, and it is strongly expressed during winter in buds, clearly suggesting its participation in the seasonal control of lateral bud outgrowth [26].

In temperate regions, photoperiod and temperature vary enormously during the seasons, and both have long been known to influence apical and axillary plant growth [27–30]. Environmental factors regulate plant growth and development by acting through internal factors. In trees with multiple axillary buds, it is crucial to control the number and position of the outgrowth of axillary buds during changing seasons for survival and maintenance with respect to energy source and sink balance. In the next section, we discuss the major components that are involved directly or indirectly in the seasonal control of branching in trees.

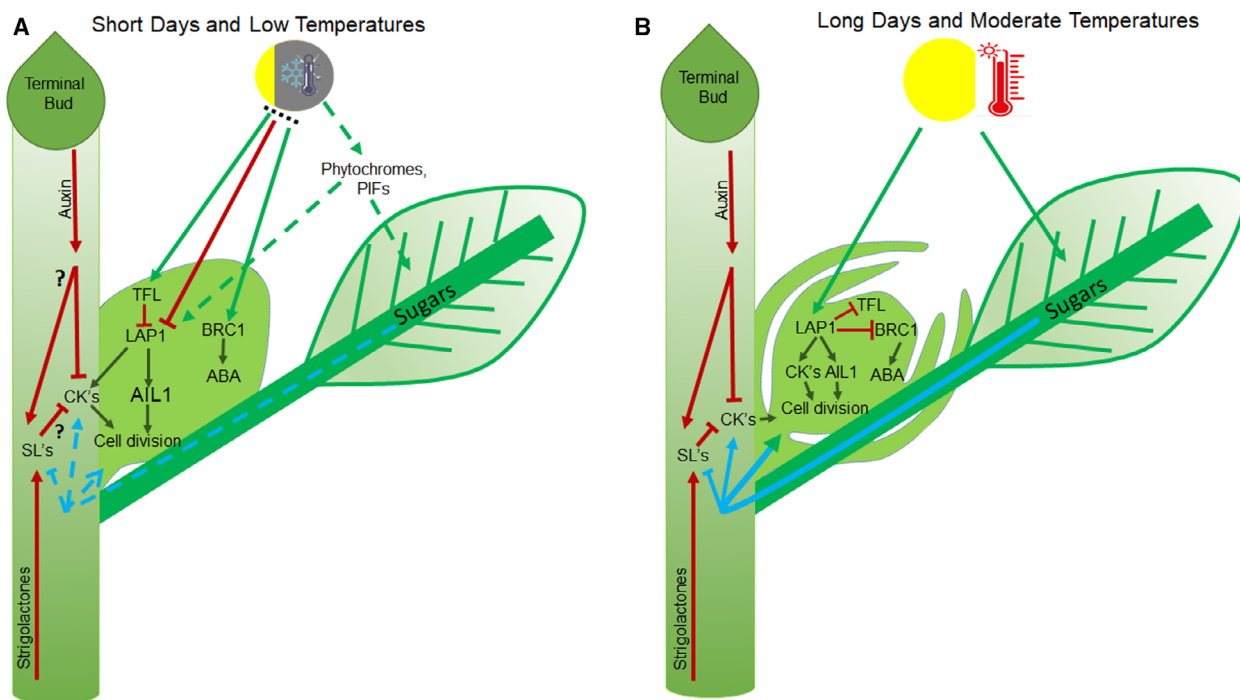
## Photoperiod and temperature control over seasonal branching in trees

Environmental factors, mainly light and temperature, are known to influence plant growth and architecture. Light is more robust, whereas, in temperate trees, temperature is also crucial and remains underexplored. Both light quality and quantity are known to affect apical and axillary bud outgrowth [27,28,31–35]. Phytochromes and cryptochromes sense light and activate

the downstream processes involved in bud outgrowth. Phytochrome B (phyB) can sense both light and temperature cues [36,37] and is known to promote branching by suppressing auxin signalling in *Arabidopsis* [38]. However, in trees, its role in branching regulation has still not been elucidated. Recently, PhyB was shown to interact with phytochrome interacting factor 8 (PIF8) and control the seasonal growth of apical meristem by acting on flowering locus T (FT) and *TFL1* in poplar plants [39], although how the *phyB* and *phyB-PIF8* module regulates lateral bud growth in perennial plants is unknown and will be interesting to investigate in the future in the context of seasonal growth.

Downstream of photoreceptors, the constans-flowering locus T (CO-FT) module plays a key conserved regulatory role in many pathways, such as flowering, tuber formation and the seasonal control of apical growth in perennial plants [4,40]. Very recently, a genetic framework responsible for the regulation and

seasonal adaptation of shoot architecture has been described in hybrid aspen trees [41]. This suggests that the *CO-FT* module does not appear to be crucial for lateral bud outgrowth because *FT*-overexpressing (*FToe*) plants do not produce more branches than wild-type plants [25]. Instead, in the seasonal control of lateral bud growth, a recently described module consisting of antagonistic players terminal flower 1 (*TFL1*) and like-apetala 1 (*LAP1*) appears to be more important than *CO-FT* (Fig. 1). *TFL1* is a negative regulator of flowering and growth and hence an antagonist of *FT* [42,43]. Unlike *FT*, the primary function of *TFL1* is to keep plant growth suppressed. *TFL1* expression is induced in lateral buds in response to short photoperiods in autumn and lower temperatures than those occurring during the long summer days of the growing season, consolidating its negative effect on lateral bud outgrowth. Plants in which *TFL1* is down-regulated produce significantly more branches than



**Fig. 1.** Seasonal control of branching: axillary bud outgrowth in temperate trees. (A) During winter, when plants experience short days and low temperatures, a seasonal repressor module operates in axillary buds that helps them remain in the dormant/non-growing stage. The module consists of *TFL-LAP1-BRC1* and their downstream components. Short photoperiods induce the expression of *TFL1*, which restricts expression of *LAP1*, a growth-promoting TF. Downstream *LAP1* promotes expression of *AIL1* and cytokinin biosynthesis genes, which regulate cell division. Simultaneously, short photoperiods induce expression of *BRC1*, a central branching regulator, which participates in the regulation of ABA biosynthesis, signalling and maintenance of the ABA levels required to maintain dormancy. (B) Following the return of summer and accompanying increases in day length (long days) and temperatures, expression of *LAP1* increases, which suppresses the negative regulators of growth, *TFL* and *BRC1*. Simultaneously, *LAP1* promotes increases in *AIL* expression and cytokinin levels, leading to activation of cell division and axillary bud outgrowth. The roles of sugars and hormones (most importantly auxin and strigolactones) in the seasonal branching of temperate trees are not well understood, and so their depiction is based on information from other plant systems.

wild-type counterparts. By contrast to *TFL1*, *LAPI* is a positive regulator that promotes apical and lateral bud growth [5,41]. *LAPI*-overexpressing (*LAPIoe*) plants are insensitive to short photoperiod and low-temperature seasonal cues. They also produce branches at almost every node. Genetic evidence suggests that *LAPI* acts downstream of *TFL1* because *LAPI* expression is enhanced in lateral buds of *TFL1-RNAi* plants (i.e. with *TFL1* expression suppressed by RNA interference). Furthermore, knocking out *LAPI* in these plants suppresses their branching phenotype. Although the branching phenotype of both *TFL1-RNAi* and *LAPIoe* plants is suppressed by short photoperiods and low temperatures, it is restored in *TFL1-RNAi/LAPIoe* plants (Fig. 1). These findings suggest that, to overcome the effects of unfavourable seasonal cues, downregulation and upregulation of *TFL1* and *LAPI*, respectively, is required. This fine-tuning of *TFL1* and *LAPI* expression could have significant applications.

Another critical player downstream of *LAPI* is *antegenitallike1* (*AIL1*), which plays an important role in seasonal control of apical growth [44]. *AIL1* expression in apical and lateral buds is reduced under short-photoperiod and low-temperature conditions [25,44]. *AIL1* promotes branch development because lines overexpressing *AIL1* and lines in which its function is suppressed (by SRDX domain-mediated repression) produce more and fewer branches than their wild-type counterparts, under long-photoperiod conditions, respectively (Fig. 1). Thus, placing *AIL1* expression under the control of short-photoperiod-inducible promoters could be potentially useful for developing crops and plants with longer growing periods, thereby extending the environments in which they can complete their life cycles during cultivation and/or provide products such as fruits. Reductions in levels of CKs and *AIL1* in short-photoperiod and low-temperature conditions probably affect the expression of key cyclin genes required for cell division. *AIL1* directly interacts with the promoter of *CYCD3.2*, a D-type cyclin gene, and promotes its expression, thereby delaying short-photoperiod-induced apical growth cessation [25,44]. Such a molecular mechanism may also be involved in the control of branching via lateral buds.

## Hormonal regulation of shoot branching

Seasonal environmental factors activate axillary buds to form branches interactively with endogenous factors, especially hormones. Major hormones involved in the process include auxins, CKs, SLs and, to some extent, GAs. Generally, auxins and SLs inhibit shoot

branching, whereas CKs promote axillary bud outgrowth [9]. Auxins are the first and most important hormone identified in shoot branching regulation, whether it be apical dominance or seasonal regulation. To date, the polar auxin transport mechanism comprises one of the most extensively studied models for branching regulation. Auxins are polarized toward the root through the xylem parenchyma and are known to suppress cytokinin (in buds) and upregulate strigolactone biosynthesis (in roots). This mechanism of action of auxin in the control of axillary bud growth has been elucidated in herbaceous plants, although how it works in trees of larger size still needs to be deciphered.

The role of CK in promoting axillary bud outgrowth has been established for a long time in annuals and herbaceous plants [9,10,45], as well as recently in trees [25]. They promote plant growth by promoting cell division and also participate in axillary bud release from dormancy. CK levels decline in short-photoperiod conditions, thereby inducing faster growth cessation in apical buds. Similarly, CKs and components of CK signalling pathways decrease in response to short photoperiods and low temperatures, leading to a reduction in the frequency of lateral bud outgrowth, and hence branch formation [41]. In addition, a reduction in cytokinin levels significantly suppresses the highly branching phenotype of *LAPIoe* plants, confirming that they are important downstream participants in the seasonal control of shoot branching in trees (Fig. 1). Similarly, the antagonistic role of SLs in shoot branching has been more intensively investigated in herbaceous plants than in trees. Mutations causing deficiency in SL biosynthesis induce profuse branching in *Arabidopsis* and other annual plants. The negative function of SLs in shoot branching in perennials is also conserved. Downregulation of SL biosynthesis gene *MAX4* in poplar using an artificial microRNA silencing approach leads to a change in shoot architecture as a result of the production of more branches [24]. Furthermore, a CRISPR/Cas9 knockout line of another SL biosynthesis gene carotenoid cleavage dioxygenase 8 also forms more branches than the control plant [15]. In herbaceous plants, SLs are synthesized in roots and travel acropetally towards axillary buds, whereas, in trees, they are reportedly synthesized and supplied to axillary buds via nodes rather than roots [46].

Abscisic acid (ABA) and GAs act antagonistically during dormancy and bud break. GA-deficient mutants are dwarf and bushy, suggesting that GAs play an inhibitory role in shoot branching in annuals and perennials. By contrast to annuals, a bud outgrowth-promoting GA function has been proposed in perennial hybrid aspen plants. Different GAs have



different proposed activities in axillary bud outgrowth, particularly GA3 and GA4, which putatively inhibit and promote the process, respectively [46]. The plant hormone ABA has been shown to have inhibitory effects on plant apical growth [7,47,48]. Similar to GA, no direct role of ABA has been confirmed in shoot branching, although there are indications that it is indirectly involved in the process in Arabidopsis. *BRC1*, a branching inhibitory transcription factor in Arabidopsis, represses lateral bud growth by promoting the expression of some ABA biosynthesis and signalling genes, such as *NCED3*, *HB21*, *HB40* and *HB53* [49]. Because the expression of these genes is also induced by short photoperiods and low temperatures in lateral buds of hybrid aspen, these two modes of ABA action could also be involved in lateral bud outgrowth.

### Sugars: signalling molecules or simply energy sources in branching regulation?

Sugars are the primary sources of energy for metabolic processes, and sucrose is considered to act as a mobile signal in diverse developmental processes in plants [50,51]. In shoot branching, sugar signals are more strongly involved in activation of dormant buds than in seasonal growth, sugar fluxes can mimic decapitation effects, and sugars rapidly accumulate in axillary buds after decapitation [33]. A recent study showed that the overexpression of the peach Early bud-break 1 (*PpEBB1*) gene in poplar leads to the formation of more branches by differentially regulating the genes and proteins involved in light response, brassinosteroid signalling and nitrogen metabolism [17]. Further analysis of *PpEBB1oe* plants also revealed the accumulation of various sugars, such as fructose, glucose, sucrose, trehalose and starch, which were correlated with an increased number of branches. In addition, areas of photosynthetic tissues (and photosynthetic rates) are positively related to sugar production in leaves and bud outgrowth, clearly indicating positive feedback effects between sugar production and bud outgrowth: increases in sugar production result in more and longer branches, and vice versa. These relationships have been well established in herbaceous plants, although they require further confirmation in trees and other perennials. However, the production of new branches in trees clearly occurs in favourable growth conditions, with long photoperiods and moderate temperatures, suggesting that similar mechanisms are involved.

Dormant axillary buds have low sugar contents and, to initiate their outgrowth, they must compete for

sugars. Moreover, their sugar acquisition is apparently related to their growth relative to that of other buds along the same axis in many perennials, although this still needs validation [52]. Similarly, in *A. alpina*, axillary bud growth zones are putatively controlled by vernalization, and sugars may play a role in the process that warrants attention. In herbaceous plants such as pea, rose and Arabidopsis, sugars interact with hormones in the regulation of axillary bud activation and branch outgrowth. Increases in sugar levels in axillary buds result in auxin efflux and simultaneous suppression of SL biosynthesis genes [10]. Conversely, phytohormones can also regulate sugar levels in various organs. In the absence of apical dominance, sugars are re-distributed to the lateral buds, which in turn suppresses the expression of *BRC1*, a key transcriptional regulator responsible for maintaining bud dormancy, thereby promoting lateral bud growth [53]. Thus, multiple physiological networks (and environmental factors) are involved in controlling sugar levels during plant development. Overall, studies to date indicate that sugars are not only energy sources, but also act as signalling molecules (especially sucrose) in the initial activation of axillary bud outgrowth. During this activation, increases in trehalose-6-phosphate levels and activities of hexokinases, which act as sucrose sensors, are consistent with indications that sucrose acts as a mobile signal in the regulation of shoot branching.

### Conserved but different molecular regulation in apical versus axillary meristem genes with divergent roles

Apical/terminal buds are very similar to axillary buds, and both enclose shoot apical meristems. Axillary bud outgrowth in plants is regulated by multiple pathways associated with diverse developmental and environmental factors [54]. Although the growth of both kinds of buds (axillary and terminal) involves the same fundamental mechanism, their regulation has certain differences. For example, unlike apical buds, axillary buds are subject to control by apical dominance. Environmental and developmental factors also have different regulatory effects on the outgrowth of apical and lateral buds of hybrid aspen, despite great similarities, including in the expression of many meristem-specific and bud/branching-related marker genes such as centroradialislike1/terminal flower 1 (*CENL1/TFL1*), *BRC1*, *BRC2* and the SL biosynthesis gene more axillary branches 1 (*MAX1*) [55]. However, these studies have not shown how branching is seasonally regulated in poplar.

*BRC1* is a key negative regulator of branching in plants because *brc1* mutants produce significantly more

branches than wild-type plants [56]. It acts as an integration point for the multiple pathways involved in branching regulation [20,54]. However, a recent study has shown that *BRC1* expression only regulates bud activation potential and is not necessary and sufficient for inhibiting bud growth in *Arabidopsis* [57]. The negative functional role of *BRC1* in branching is also conserved in higher perennial plants. Lines with *BRC1* or its close homologue *BRC2* knocked out by CRISPR-Cas9 genome editing reportedly produce more branches than their respective wild-type plants [24]. *BRC1* homologue in grapevine (*VvBRC1*) also inhibits branch formation by differentially regulating the transcript levels of the ABA pathway and cell cycle-related genes [16]. *VvBRC1* inhibits branch formation by promoting the transcripts of *ABF3*, *ABI5*, *HB21*, *HB40* and *HB53* at the same time as downregulating the expression of *CYCD3* and *HISTONE H4* genes. Very recently, it was also found that *BRC1* is involved in seasonal regulation of apical growth in hybrid aspen plants [41], suggesting that it plays divergent roles in different tissues. This seasonal regulatory role of *BRC1* also appears to be conserved in lateral branches. Seasonal cues such as short photoperiods and low temperatures induce expression of *BRC1* in both apical and lateral buds, thus inhibiting their growth in unfavourable conditions. This may be a possible adaptation strategy used by perennial plants to protect their meristematic regions from the incoming future extreme cold conditions prevailing in the temperate and boreal parts of the world, during which snow injuries can kill these regions. By protecting these meristematic regions, plants ensure their potential growth in the upcoming spring and summer seasons, during which *BRC1* expression declines. Targeting *BRC1* to modulate plant branching phenotypes could have immense biotechnological and agricultural importance. Keeping the *BRC1* level low will generate plants with fewer branches, which could be helpful for timber industries. Conversely, genes that promote lateral bud growth could be overexpressed or expressed in lateral buds under the control of promoters such as *BRC1* promoters to induce more bud growth and obtain profusely branched plants. These strategies could enhance the production of fruits and other edible products from plant shoots.

## Conclusions and future perspectives

Shoots have strong architectural plasticity, adopting myriads of shapes and forms in response to developmental signals associated with diverse endogenous and exogenous factors, including natural seasonal cues.

Antagonistic players *TFL1* and *LAPI* are key regulators of the growth of perennial plant lateral buds in these responses. Other players such as CKs, *AIL1*, *BRC1* and ABA act downstream of the *TFL1-LAPI* regulatory module. Overall, a complex network of biochemical and molecular players seasonally fine-tune the growth of plant lateral buds. In the future, it should be possible to engineer and develop perennial plants with socio-economically desirable features using combinations of genetic and modern biotechnological advances. For example, knowledge obtained from studies of the seasonal regulation of branching could be used to engineer single-stemmed trees or trees with minimal branches, as preferred by timber-processing industries. Such strategies could also be used to modulate plant biomass and develop more plants such as columnar apple trees, which can be grown and provide edible fruits in gardens or buildings with less space than conventional apple trees require. Conversely, more profusely branched plants capable of providing more edible and other valuable materials in broader environmental conditions than current crops (and hence potentially cope with anticipated environmental changes) can be developed to support increasing global demands. Furthermore, combining knowledge from studies of annual and perennial plants could strongly help efforts to meet urgent needs to develop more climate-smart perennial plants with socio-economically valuable traits.

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## Conflicts of interest

The authors declare that they have no conflicts of interest.

## Author contributions

RKS, RPB and JPM wrote the manuscript.

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