

# Regulation of axillary shoot development

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Axillary meristems are formed in leaf axils and their growth into branches is a highly controlled process that is an important contributor to plant architecture. Here we discuss work that improves our understanding of the initiation and growth of axillary meristems. Recent results have implicated brassinosteroid signalling in the formation of axillary meristems. Our knowledge of axillary meristem outgrowth has also advanced, particularly in the areas of strigolactone signal production and perception, which have been shown to respond to environmental inputs. Auxins and cytokinins have also been linked to the control of axillary shoot development, revealing a complex network of signals that combine to regulate the outgrowth of an axillary meristem into a branch.

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## Introduction

Branching in plants is a highly regulated process, with inputs from environmental and developmental pathways integrated into the regulation of axillary meristem formation and outgrowth (Figure 1). While common branching patterns exist, many species display a unique architecture, with subtle variations on themes resulting in distinct patterns of growth. The roles of auxin, cytokinin (CK) and strigolactones (SLs) in branch formation are well established [1–6]. In this review we will first consider recent work identifying brassinosteroid (BR) signalling as a component of axillary meristem formation. We will then examine in detail recent results that increase our understanding of SL biosynthesis and perception. This progress has allowed some understanding of the evolution of the SL pathway and its possible roles in ancestral plants. In addition, work in multiple species has revealed connections between environmental signalling pathways and the hormone pathways that result in branching.

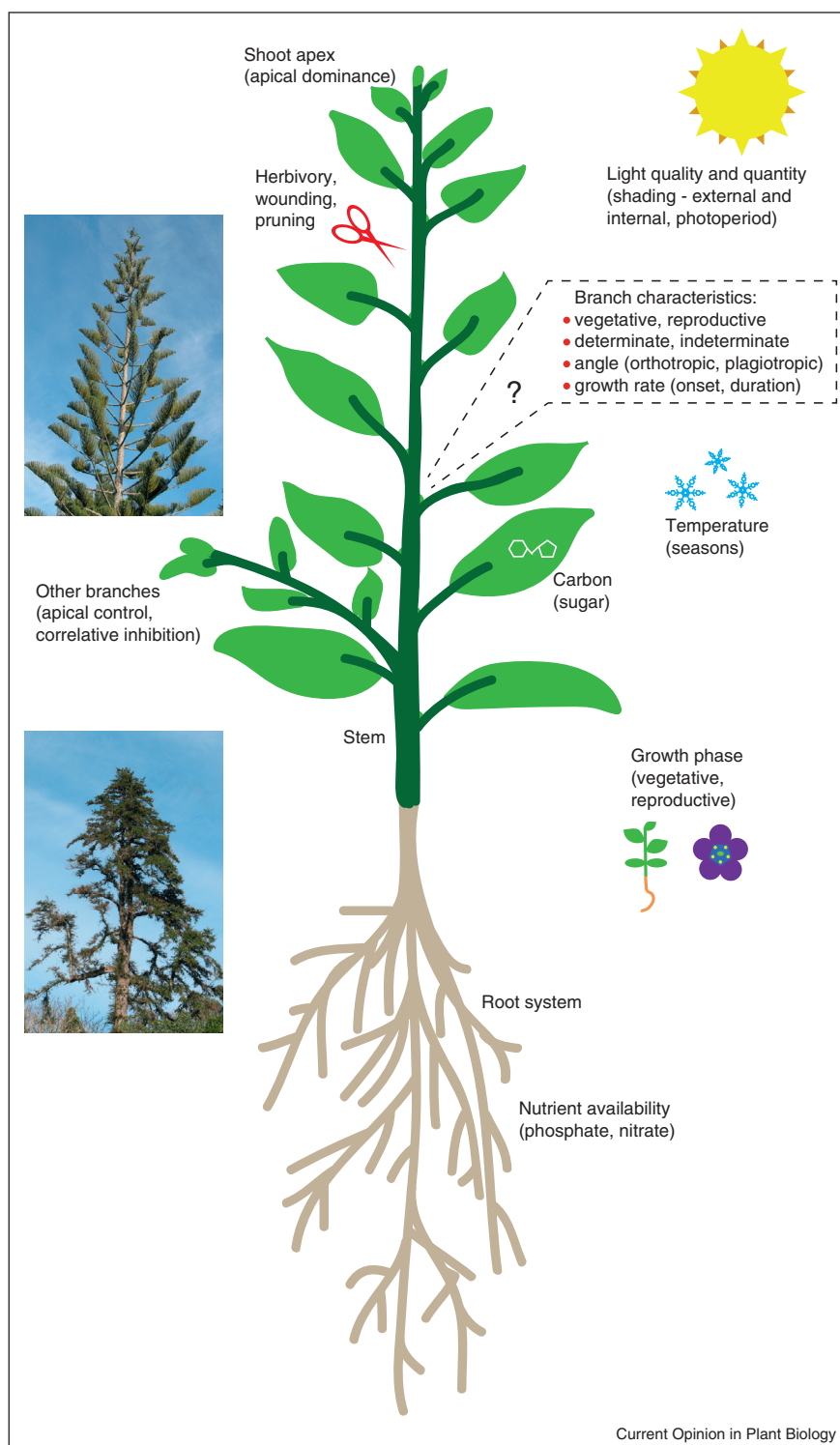
## Axillary meristem initiation

The production of axillary meristems is tightly linked to the production of leaves and their separation from the shoot apex. As leaf primordia are formed on the flanks of the shoot apical meristem, a region of small, slowly dividing cells develops between the apex and the developing organ, forming a boundary zone. It is within this zone that axillary meristems form. After axillary meristems are formed they can grow or enter a dormant state, often forming a bud with a number of nodes.

A set of transcription factors, largely identified from screens for organ fusion and axillary meristem mutants, have been implicated in the specification of the boundary zone. These include R2R3 MYBs (LATERAL ORGAN FUSION1 (LOF1) and REGULATOR OF AXILLARY MERISTEMS (RAX) from *Arabidopsis* and the RAX homologs BLIND (Bl) and POTATO LEAF (C) from tomato; NAC domain proteins CUP-SHAPED COTYLEDON1-3 (CUC1-3) from *Arabidopsis* and the tomato ortholog GOBLET (Gob); a GRAS domain protein (known as LATERAL SUPPRESSOR (Ls) in tomato, LAS in *Arabidopsis* and MONOCULM1 (MOC1) in rice); a bHLH protein (LAX PANICLE1 (LAX1) from rice, BARREN STALK1 (BA1) from maize and REGULATOR OF AXILLARY MERISTEM FORMATION (ROX) from *Arabidopsis*), and a LBD protein (LATERAL ORGAN BOUNDARIES (LOB) from *Arabidopsis*), with many of these proteins apparently acting redundantly to specify boundary zone identity [7,8–10].

An analysis of the targets of LOB found that a high percentage of these genes had previously been identified as BR modulated. Of particular note was that within the boundary zone LOB acts to increase the abundance of PHYB ACTIVATION TAGGED SUPPRESSOR1 (BAS1), a gene encoding a BR-catabolising enzyme [7]. In addition, the BR-activated transcription factor BRASSINAZOLE-RESISTANT1 (BZR1) has been shown to repress the *CUC* genes directly [11]. Hence the lowered BR content achieved by the LOB-dependent activation of BAS1 leads to a decrease of BZR1 and thereby an increase in *CUC* and *LOF1* transcripts (reviewed in [8]). In *Arabidopsis*, mutations in the *LOF1* gene have lateral organ fusions [12], whereas in tomato the orthologous *trifoliolate* (*tf*) mutants have been shown to have reduced leaf complexity as well as loss of axillary branching [13]. The *tf* result extended an earlier observation that in tomato, Bl, C, Ls and Gob are involved in both leaflet and axillary meristem formation [14]. With the identification of reduced BR signalling, these data reinforce the idea that the boundary zone consists of cells

Figure 1



Overview of factors influencing plant branching. The branching component of plant architecture is dependent on the position of meristems in the plant, the timing of their growth (e.g. as a seasonal process or during vegetative or reproductive growth phases), and the characteristics of the branch. A number of plant organs contribute to the control of axillary meristem outgrowth, including the shoot apex, other branches, the stem and roots of the plant. The plant also integrates signals from environmental stimuli, including light and nutrients. Overall plant shape can be achieved in different ways (see inset photographs that show two related gymnosperm trees with very regular, simple branches (top) or more irregular, compound branches (bottom)) with differing emphasis on varying combinations of developmental programmes and environmental cues.

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