



## Review

## Stem cell function during plant vascular development

A. Elo<sup>a</sup>, J. Immanen<sup>a</sup>, K. Nieminen<sup>a,1</sup>, Y. Helariutta<sup>a,b,\*</sup><sup>a</sup> Department of Biological and Environmental Sciences, Institute of Biotechnology, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland<sup>b</sup> Department of Forest Genetics and Plant Physiology, Umeå Plant Science Center, Swedish University of Agricultural Sciences, 90183 Umeå, Sweden

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## ABSTRACT

While many regulatory mechanisms controlling the development and function of root and shoot apical meristems have been revealed, our knowledge of similar processes in lateral meristems, including the vascular cambium, is still limited. Our understanding of even the anatomy and development of lateral meristems (procambium or vascular cambium) is still relatively incomplete, let alone their genetic regulation. Research into this particular tissue type has been mostly hindered by a lack of suitable molecular markers, as well as the fact that thus far very few mutants affecting plant secondary development have been described. The development of suitable molecular markers is a high priority in order to help define the anatomy, especially the location and identity of cambial stem cells and the developmental phases and molecular regulatory mechanisms of the cambial zone. To date, most of the advances have been obtained by studying the role of the major plant hormones in vascular development. Thus far auxin, cytokinin, gibberellin and ethylene have been implicated in regulating the maintenance and activity of cambial stem cells; the most logical question in research would be how these hormones interact during the various phases of cambial development.

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\* Corresponding author at: Department of Biological and Environmental Sciences, Institute of Biotechnology, University of Helsinki, P.O. Box 65, 00014 Helsinki, Finland.

E-mail addresses: [annakaisa.elo@helsinki.fi](mailto:annakaisa.elo@helsinki.fi) (A. Elo), [juha.immanen@helsinki.fi](mailto:juha.immanen@helsinki.fi) (J. Immanen), [kaisa.nieminen@helsinki.fi](mailto:kaisa.nieminen@helsinki.fi) (K. Nieminen), [yrjo.helariutta@helsinki.fi](mailto:yrjo.helariutta@helsinki.fi) (Y. Helariutta).<sup>1</sup> Present address: University of Lausanne, Department of Plant Molecular Biology, Biophore Building, CH-1015 Lausanne, Switzerland.

## 1. Introduction

Plant vascular tissues serve two main functions: they give physical structure and support, and deliver water, nutrients and other substances needed for growth and defence. Vascular tissues connect all parts of the plant, from the root system through the stem into the leaves. The exact pattern the vascular tissues are arranged in the plant is diverse and dynamic, depending on the taxonomic position of the species. In many gymnosperms and dicotyledonous angiosperm plants, two distinct phases of vascular development are recognized: primary and secondary. During primary development in leaves, stems and roots the vascular tissues form bundles which consist of two fully differentiated, conductive tissue types, xylem and phloem, with intervening procambial pluripotent cells. During secondary development in stems and roots, the vascular pattern is further elaborated to eventually form concentric rings of xylem (in the centre), cambium and phloem.

Whereas xylem and phloem are the conductive tissues, procambium and cambium refer to the intervening pluripotent cells that are able to form the two tissue types based on asymmetric periclinal cell divisions (cell division plane parallel to plant surface). At the moment we lack precise developmental understanding of the transition from procambium to cambium. Thus, it seems appropriate to use the general term “vascular meristem”, which collectively covers the various developmental phases of this pluripotent tissue type. Proliferating cambial cells form a source for differentiating xylem (wood) and phloem cells and cambial activity leads to a thickening of the stem and, concomitantly, to an increase in biomass. The activity of the vascular cambium (or secondary growth) is particularly profound in woody plants (trees), since the wood in tree trunk originates from the proliferative activity of the vascular cambium. Therefore, the lateral meristem research has been traditionally focusing on tree species. However, activity of the vascular cambium and secondary growth are also crucial for many herbaceous plants. Accordingly, *Arabidopsis thaliana* has emerged as a useful model for analysing this phenomenon (e.g. [1–7]); in particular, the *Arabidopsis* root has proven to be an excellent model for studying secondary development in higher plants.

As discussed above, vascular pattern is diverse and dynamic. Concerning the variation within an individual, the vascular pattern differs during leaf, stem and root development. This diversity of patterns reflects the different status of local or global signals or environmental stimuli, one important such factor being the seasonal cycling between periods of active growth and dormancy in perennial plants.

With the rapid development of genomic and molecular tools, our knowledge regarding the regulation of vascular development, such as cambial cell proliferation and the subsequent differentiation into xylem or phloem, has been expanding rapidly, with most of the advances being made in studies on the effects of plant hormones in the development.

Several plant hormones, such as auxin, cytokinin, gibberellin and ethylene, have been implicated in the regulation of cambial activity [8,6,9,10]. While the plant hormones have been shown to play a crucial role during primary and secondary vascular development and the regulation of cell proliferation activity in the cambium, the exact signalling mechanisms are still unknown. Identification of the role of cytokinin signalling in procambial development and cambial cell proliferation has helped us to understand the formation and maintenance of stem cell populations in plant lateral meristems [11,2,12,6]. Molecular and genetic studies of *Arabidopsis thaliana* mutants, cellular studies with *Zinnia elegans* xylogenetic cultures and molecular studies of the vascular cambium in *Populus* trees have started to reveal several of other signals besides classical plant hormones and their interactions at the molecular level (e.g. [13,3,14,15]).

## 2. Development and organization

### 2.1. Primary development

During embryogenesis, the plant body is shaped by the activity of the apical meristems of the shoot and root. Vascular patterning has been studied at a cellular level for root development in *Arabidopsis*. The formation of vascular tissue is preceded by the formation of procambium in early globular stage embryos. At the late globular stage, four procambium cells divide periclinally giving rise to the pericycle and vascular primordium [16]. During the late globular, heart and torpedo stages, the number of cell files in the procambium continues to increase by further periclinal cell divisions. Simultaneously, a network of provascular or preprocambial cells forms in the cotyledons. The same process is recapitulated when lateral organs are established post embryogenesis. Soon after germination, the pre-procambial tissue is patterned as the defining domains for xylem and phloem differentiate within the procambium tissue in an organ-specific manner. In the primary vascular patterning of the *Arabidopsis* root, undifferentiated cell files separate the central xylem axis from the two phloem poles; these undifferentiated cells will later give rise to the vascular cambium (Fig. 1a). In *Arabidopsis* shoots, cambial activity starts in the fascicular cambium in the primary vascular bundles and is extended to interfascicular regions connecting adjacent bundles, leading to the formation of a closed cylinder of meristematic cells, the vascular cambium [17–19].

Although mutant analyses have provided insights into vascular patterning and the various signals controlling vascular development (reviewed, e.g. by [12,5]), our knowledge about the molecular control of vascular patterning is still relatively poor compared with other plant tissues. Plant hormones play a critical role in vascular development; in particular, auxin has been shown to trigger and maintain cambial activity and the formation of vascular strands [20,8]. It has been established that polar auxin transport is required for continuous vascular pattern formation and for the development of procambial strands [21–23]. The auxin-flow canalization theory was originally proposed by Sachs [24,20]; it suggests that the continuous polar transport of auxin through cells ultimately results in the differentiation of strands of procambial cells and, subsequently, vascular strands. During vein formation in leaves, the progenitor cells (“pre-procambial” cells) are formed from subepidermal leaf ground cells. Following the determination of vascular identity, the vascular strands are patterned and the newly formed vascular cells divide and elongate along a common axis, which is essential for the formation of a continuous vein network that can carry out its various transport roles [25,22].

Genetic studies have revealed that several genes involved in cell proliferation are downstream of auxin signalling. An auxin inducible homeobox gene, *ATHB8*, is expressed in the procambial cells of the newly forming vascular strands [26]. *PIN1* expression was shown to precede procambium formation and *AtHB8* expression during leaf vein patterning [22]. During primary development, phloem and xylem develop in an adaxial/abaxial manner in the vascular bundles. The adaxial/abaxial polarity of lateral organs and the vascular tissue of the shoot is established by the antagonistic activity of two gene families, the plant-specific class III homeodomain-leucine-zipper-containing (HD-ZIPIII) transcription factors [*PHABULOSA* (*PHB*), *REVOLUTA* (*REV*), *PHAVOLUTA* (*PHV*), *CORONA* (*AtHB15*) and *AtHB8*] and the *KANADI* [*KAN1-3*] GARP transcriptional regulators [27–33]. Mutations in the auxin regulated gene *REVOLUTA* (*REV*, described earlier as *INTERFASCICULAR FIBERLESS1* or *IFL1*) resulted in the absence of interfascicular fibers in the stem and disrupted development of xylem fibers and vessel elements, suggesting a role for the corresponding gene during secondary development [34,35]. Xylem differentiation and

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