Journal of Plant Biology, June 2007, 50(3) : 301-305 **REVIEW**

Vascular Development in Plants: Specification of Xylem and Phloem Tissues

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The plant vascular system is a complicated network of conducting tissues that interconnects all organs and transports water, minerals, organic compounds, and various signaling molecules throughout the entire organism. This system is composed of two major tissue types – xylem and phloem – that originate from the vascular meristem, i.e., the procambium. Recently, combined applications of molecular genetics and genomics tools have provided significant insights into the underlying mechanisms by which specification of these two types are regulated. They include 1) the asymmetric patterning of xylem and phloem in the vascular bundle that arises through antagonistic functioning between the HD-ZIP III and KANADI transcription factors, 2) control of vascular cell proliferation by brassinosteroids (BRs) and the HD-ZIP III transcription factors, and 3) regulation of vascular tissue identity by the MYB transcription factor APL and the NAC transcription factors VND6 and VND7. These findings define an emerging developmental framework for the control of vascular tissue specification.

Keywords: brassinosteroid, HD-ZIP III, microRNA, phloem, vascular system, xylem

TRANSITION OF PLANTS TO TERRESTRIAL HABITATS

Plant colonization on land may have occurred as early as the Silurian period some 430 million years ago. To achieve a successful transition from aquatic to terrestrial habitats, plants invoke mechanisms for protection against water loss, absorption of water and nutrients from the soil, transfer of assimilates throughout the entire organism, and mechanical support. The vascular tissues provide long-distance transport of water and nutrients as well as sufficient rigidity. In primitive vascular species, those tissues are organized in a simple fashion, such that xylem is located at the center and is surrounded by phloem. In diverse vascular plants, those systems possess a variety of structural and functional organizations (Ye, 2002; Scarpella and Meijer, 2004).

In this review, we briefly describe the structural aspects of a plant vascular system, and summarize the recent findings from studies that have identified the molecules or signaling pathways involved in vascular development. For more in-depth understanding of other aspects of this topic, including procambial organization and secondary growth, we encourage readers to refer to other recent reviews (Ye, 2002; Fukuda, 2004; Scarpella and Meijer, 2004; Carlsbecker and Helariutta, 2005; Sieburth and Deyholos, 2006).

THE PLANT VASCULAR SYSTEM

In higher plants, vascular tissues play essential roles that range from physiological (transport of water and nutrients) to developmental (transfer of signaling molecules), to architectural (physical support). A typical system contains two basic units, xylem and phloem. Xylem moves and stores water and nutrients, transports diverse plant hormones (e.g., abscisic acid and cytokinin), and lends major mechanical support. Phloem provides passageways for the distribution of photosynthetic products, such as sucrose, and for translocating the proteins and mRNAs involved in growth and development. Both xylem and phloem usually comprise a number of specialized vascular cell types, including conducting elements (tracheary elements in the xylem and sieve elements in the phloem), parenchyma, and sclerenchyma cells.

Xylem and phloem are differentiated from a distinct type of meristematic tissue – the procambium and vascular cambium – to form vascular bundles that connect all parts of the plant body (Fig. 1A). During the primary growth of stems and roots, procambial cells derived from apical meristems produce xylem and phloem precursor cells. The latter subsequently differentiate into various phloem cells, such as the sieve elements (SEs), companion cells (CCs), phloem parenchyma cells, and phloem fibers. Xylem precursor cells give rise to tracheary elements (TEs), xylem parenchyma cells, and xylem fibers, which together comprise the xylem. TEs are essential components in a vessel. After maturation, they are emptied by the loss of all cellular contents, including the nucleus, to form hollow tubes through which fluids move. They possess a characteristic secondary cell wall of annular, spiral, reticulate, or pitted wall thickenings, which provide additional strength and rigidity and prevent the TEs from collapsing under the high pressure that is frequently exerted upon fluid uptake.

PROCESSES OF VASCULAR DIFFERENTIATION

Vascularization is initiated by the formation of provascular

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Abbreviations: ATHB8, *Arabidopsis thaliana* Homeobox 8; CAN, CORONA; HD-ZIP III, class III homeodomain-leucine zipper; miRNA, microRNA; PHB, PHABULOSA; PHV, PHAVOLUTA; REV/IFL1, REVOLUTA/INTERFASCICULA FIBERLESS1; SAM, shoot apical meristem; START, StAR-related lipid-transfer cells that later develop into procambium, from which both conducting tissues are eventually differentiated (Steeves and Sussex, 1989; Kang and Soh, 2001). In older plant parts, vascular tissues can be formed through the activity of a secondary meristem, called the vascular cambium (Esau, 1965; Albert and Shah, 2006). Plant growth hormones, such as auxins and brassinosteroids (BRs), play regulatory roles in this differentiation (Jang et al., 2000; Sachs, 2000; Carland et al., 2002). It is now widely accepted that a unified molecular mechanism modulates temporal and spatial regulation of vascular tissue development in various species, although their detailed patterns and organizations are quite diverse (Baima et al., 2001). However, their molecular components and control schemes are only poorly understood. Recent application of versatile molecular genetics tools and genome-wide screens, mainly established in the model plant *Arabidopsis*, has greatly accelerated the identification of genes involved in that development and the elucidation of regulatory mechanisms at the molecular level. Relying of this background information, we will describe here the differentiation and radial patterning of vascular tissues, placing particular emphasis on the functioning of the Class III *HD-ZIP* gene family.

RADIAL PATTERNING OF THE VASCULAR BUNDLE

Within the vascular bundle, the xylem, procambium, and phloem exhibit a distinct dorso-ventral organization – xylem is localized on the dorsal (adaxial) side, phloem on the ventral (abaxial) side, and procambium between the xylem and phloem tissues (Fig. 1A). In shoots, this patterning is closely associated with the adaxial/abaxial patterning of the lateral organs and with the establishment of central versus peripheral identities within the stem (Engstrom et al., 2004; Fukuda, 2004). Recent studies have shown that antagonistic regulation of the Class III HD-ZIP and KANADI transcription factors is critical for this radial patterning.

MicroRNA regulation of the HD-ZIP III gene family

A subset of Class III HD-ZIP transcription factors has been implicated in vascular development. In *Arabidopsis*, the *HD-ZIP III* gene family includes five members: *ATHB8*, *ATHB15/CNA*, *PHV*, *PHB*, and *REV/IFL1*. These exhibit discrete expression domains. *PHV*, *PHB*, and *REV* are expressed in various plant parts, including the vascular tissues, apical and floral meristems, and adaxial domain of the lateral organs (McConnell et al., 2001; Otsuga et al., 2001; Emery et al., 2003). By contrast, *ATHB15* and *ATHB8* are predominantly expressed in the vascular tissues, especially in the procambial or xylem precursor region (Baima et al., 1995; Ohashi-Ito and Fukuda, 2003).

A visible, gross plant phenotype for loss-of function mutants in the *HD-ZIP III* genes has been described only for *REV* (Talbert et al., 1995; Zhong and Ye, 1999; Ratcliffe et al., 2000; Otsuga et al., 2001). The inflorescence stems of *rev* mutants lack the xylem and interfascicular layers that interconnect the vascular bundles. Despite this loss, there is no observable defect in vascular dorso-ventral patterning. The absence of functional *PHB* and *PHV* genes in a double mutant has no apparent phenotypic consequences. However, the triple mutant of *REV*, *PHB*, and *PHV* produces radially symmetrical cotyledons with an abaxialized vasculature, in which phloem surrounds xylem (Emery et al., 2003). This is in contrast to the normal collateral pattern in which phloem is found on the abaxial side and xylem on the adaxial side (Fig. 1B). Like *PHB* and *PHV*, the loss of either *ATHB8* or *ATHB15* or a combined loss has no evident phenotypic effects, although vascular development is slightly perturbed in the *athb15* mutant. However, mutations in *ATHB8* and *ATHB15* suppress the axillary and floral meristem defects observed in the *rev* mutant. Interestingly, the additional loss of *ATHB15* in the *rev* background increases the frequency of more severe phenotypic changes. The quintuple mutant, which lacks the functioning of all five *HD-ZIP III* genes, is similar to the severe *phb phv rev* mutants (Prigge et al., 2005).

Meanwhile, dominant *rev-D*, *phb-D*, and *phv-D* gain-of-function mutants possess adaxialized lateral organs and develop altered vascular bundles in which xylem surrounds phloem (Fig. 1B; McConnell et al., 2001; Emery et al., 2003; Juarez et al., 2004; McHale and Koning, 2004; Zhong and Ye, 2004). Moreover, all the gain-of-function mutations in the *HD-ZIP III* genes occur in the microRNA165 (miR165) or miR166 target sequence that resides within a putative sterol/lipid-binding (START) domain. Mutations in the miRNA target sequence that do not otherwise alter the amino acid sequences result in a similar dominant phenotype, suggesting that the *HD-ZIP III* genes are under the control of miRNA regulation (Fig. 1C; Emery et al., 2003; Mallory et al., 2004; McHale and Koning, 2004). In *Arabidopsis*, miR165/166 initially accumulates in the meristem and later in the abaxial/phloem domain of the leaf, showing a pattern complementary to that of *PHB* (Mallory et al., 2004). Similarly, expression of the maize *REV* homologue *rolled leaf1* is spatially defined by miR166 distribution (Juarez et al., 2004), further supporting the miRNA regulation of the *HD-ZIP III* genes.

KANADI

A group of KANADI (KAN) proteins that belong to the GARP-type transcription factors also play important roles in vascular development. The *kan1 kan2 kan3* triple mutant develops abnormal bundles in which xylem surrounds phloem [like the *rev-D*, *phb-D*, or *phv-D* gain-of-function mutants], and the pattern of *HD-ZIP III* expression is also abaxialized (Fig. 1B). Furthermore, localized expression of *KANADI* in the phloem and in the abaxial leaf domain is reminiscent of the localization of miR165/166 (Eshed et al., 2001, 2004; Kerstetter et al., 2001; Emery et al., 2003). These observations reflect the antagonistic roles of the HD-ZIP III and KANADI proteins in xylem and phloem patterning within the stem (Fig. 1C). However, even though both *HD-ZIP III* and *KAN* are also expressed in the roots in a complementary pattern, there is no phenotypic evidence from the mutants to support a role for either the *HD-ZIP III* genes or the *KAN* genes in patterning regulation of the root vascular bundles (Hawker and Bowman, 2004).

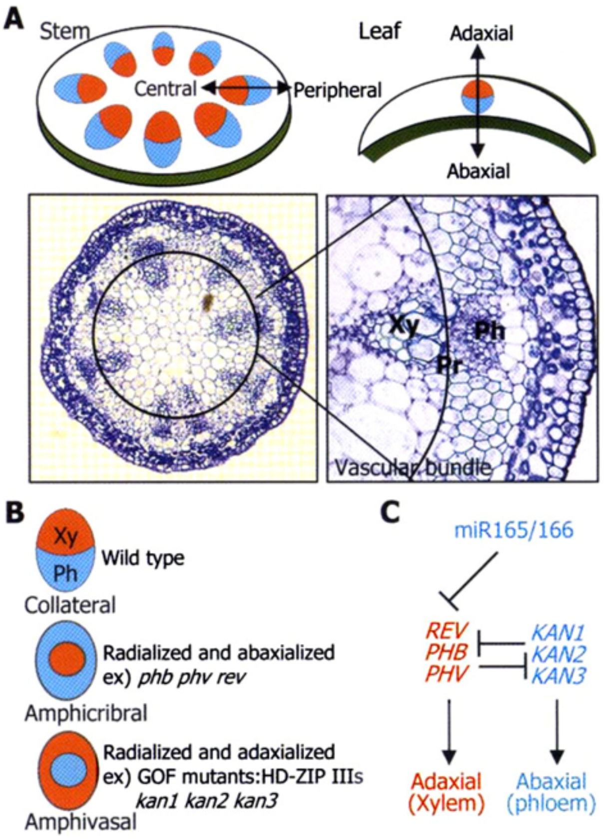

Figure 1. Vascular pattern formation. (**A**) The vascular system consists of phloem (Ph), procambium (and/or vascular cambium; Pr), and xylem (Xy), which generate a distinct radial pattern of vascular bundles. (**B**) In *Arabidopsis*, vascular tissues are organized into collateral bundles, but vascular bundles show changes in cellular organization that correspond to the polarity shift. (**C**) A model illustrating how activities of HD-ZIP III and KANADI regulate pattern vasculature (Emery et al., 2003).

CONTROL OF XYLEM AND PHLOEM CELL PROLIFERATION

HD-ZIP III gene family and microRNA

Molecular genetic data have indicated a critical role for the *Arabidopsis HD-ZIP III* genes during vascular tissue cell proliferation. *ATHB8*, induced by auxin, promotes cell proliferation and xylem differentiation (Baima et al., 2001). However, a loss-of-function *athb8* mutant does not exhibit any visible defects in this patterning and development, suggesting that this gene is a positive regulator of, but not essential to, vascular proliferation and differentiation (Baima et al., 2001; Prigge et al., 2005). Two semi-dominant mutants – *meristem enlargement1* (*men1*) and *jabba-1D* (*jab-1D*) – have now been isolated through the screening of *Arabidopsis* activation-tagged mutant lines (Kim et al., 2005; Williams et al., 2005). Overexpression of the *MIR166a* or *MIR166g* genes results in reduced amounts of transcript for *HD-ZIP III* in the mutants. The *ATHB15* transcript also is predominantly diminished in *men1*/+. This is accompanied by the over-proliferation of xylem tissue and interfascicular fibers in the stems of both *men1*/+ and *jab-1D* mutants (Fig. 2B). Transgenic plants with decreased *ATHB15* expression are severely dwarfed, with fasciated inflorescence stems similar to those of the *men1*/+ mutants (Fig. 2B). Expansion of lignified tissues is significantly promoted in the antisense *ATHB15* transgenic plants, and the number of vascular bundles also is influenced (Kim et al., 2005). Together with the distinct procambial expression of *ATHB15* (Ohashi-Ito and Fukuda, 2003), it is obvious that, unlike *ATHB8*, this gene is critical for vascular development, negatively regulating cell differentiation. Therefore, these two paralogues – *ATHB8* and *ATH15* – might act antagonistically to control the proliferation of vascular tissue in relation to xylem development. Both are post-transcriptionally regulated by miR166 through mRNA cleavage. Altogether, these observations suggest that miR166/165 might be a modulator that balances the functioning of *ATHB15* and *ATHB8* during vascular development (Kim et al., 2005).

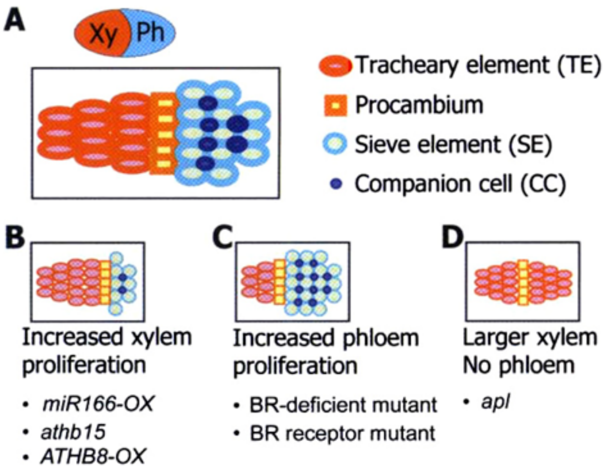

Figure 2. Schematic representation of xylem and phloem cell proliferation. (**A**) Within the vascular bundles, phloem precursor cells differentiate into various phloem cells, such as sieve elements (SEs) and companion cells (CCs), whereas xylem precursor cells give rise to tracheary elements (TEs). Processes that regulate this vascular bundle patterning have been revealed by analyses of several vascular-tissue-proliferation mutants (**B**, **C**), and one vascular-tissue-identity mutant (**D**).

Brassinosteroids

Several growth hormones have been demonstrated or implicated in vascular tissue formation and differentiation. The importance of BRs has been recently confirmed from observations of reduced xylem and increased phloem development, which evidently result from the disruption of several BR receptor kinase genes -- *BRASSINOSTEROID INSENSITIVE 1* (*BRI1*), *BRI1-LIKE1* (*BRL1*), and *BRI1-LIKE3* (*BRL3*) (Caño-Delgado et al., 2004). BRL1 and BRL3 were identified on the basis of their sequence similarities to the previously identified BRI1 receptor, a leucine-rich repeat receptor kinase that directly binds BRs (Wang et al., 2001; Kinoshita et al., 2005). The *BRI1* gene is ubiquitously expressed in dividing and elongating cells, whereas the *BRL1* and *BRL3* genes are expressed predominantly in vascular tissues, with *BRL3* specifically expressed in the phloem. Furthermore, analysis of the *bri1 brl1 brl3* triple mutant has led us to suggest that these may act redundantly in regulating vascular differentiation (Fig. 2C). It is possible that signaling through the BR receptors in the procambium induces xylem proliferation while simultaneously repressing phloem proliferation.

An *HD-ZIP III* gene encoding an *Arabidopsis ATHB8* gene homolog is mainly expressed in the xylem cells, and induced by BRs in cultured *Zinnia elegans* cells (Ohashi-Ito et al., 2002). Consistent with this, xylem development is reduced in BR-deficient *Arabidopsis* (Fig. 2C; Choe et al., 1999). Brassinazole (Brz), a potent BR biosynthesis inhibitor, represses xylem formation (Nagata et al., 2001), further supporting a role for BRs. *ZeHB-13*, an *ATHB15* gene homolog in *Z. elegans*, is suppressed by Brz but restored by the addition of BR, indicating that BR is not required for *ZeHB-13* induction but does promote its expression (Ohashi-Ito and Fukuda, 2003). These results suggest that the *HD-ZIP III* genes function in vascular differentiation in response to BR signals. Moreover, it is still possible that auxin signals are also incorporated into this regulatory scheme.

APL, VND6 and VND7

A few genes have been shown to exert direct effects on phloem cell identity. Among these, the best understood are three putative transcription factor genes -- *ALTERED PHLOEM DEVELOPMENT* (*APL*; which encodes an MYB coiled-coil transcription factor), *VASCULAR-RELATED NAC-DOMAIN6* (*VND6*), and *VND7* (Bonke et al., 2003; Kubo et al., 2005). For example, loss-of-function mutants of *APL* do not develop phloem SEs or CCs, and, often, instead form TEs in their place (Fig. 2D). Ectopic expression of *APL* in the vascular stele prevents or delays differentiation of the TE but is not sufficient to induce ectopic phloem differentiation (Bonke et al., 2003). These results imply that *APL* is necessary, but not sufficient, for phloem differentiation, and that *APL* is also required for inhibiting xylem differentiation in phloem positions. In contrast, loss-of-function mutants of *VND6* or *VND7* have no discernible effects on vascular development, although ectopic expression of either can cause cells as diverse as the guard cells or root endodermis to re-differentiate as cells that resemble the TEs of protoxylem (*VND7*) or metaxylem (*VND6*) (Kubo et al., 2005).

CONCLUDING REMARKS

Formation of the vascular system is a complex developmental process that must be coordinately regulated via the interactions of diverse genetic components and growth hormones. Furthermore, system patterning and organization are quite variable among species. However, the molecular mechanisms that underlie this spatial and temporal regulation are likely shared by all vascular plants. The highly conserved, fundamental architecture and the presence of *HD-ZIP III* genes in diverse species, e.g., dicots, monocots, and mosses (Floyd and Bowman, 2004), strongly support the theory that miR165/166-mediated regulation of vascular development via the *HD-ZIP III* genes is functional in all vascular plants.

It is important to note, however, that we are far from having a full understanding of the molecules and mechanistic schemes that govern vascular development. Both the complexity of overexpression phenotypes and various results from loss-of-function analyses suggest that, in order to comprehend the roles associated with specific *HD-ZIP III* genes, we must identify their direct targets. For example, the MYB transcription factor APL or the NAC transcription factors VND6 and VND7 are putative candidates, despite the current lack of direct experimental evidence. With the availability of various mutants in patterning and differentiation and the further characterization of their corresponding genes, it will soon be possible to solve the multiple questions concerning vascular development.

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