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Emergence of plant vascular system: roles of hormonal and non-hormonal regulatory networks

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The divergence of land plants followed by vascular plants has entirely changed the terrestrial ecology. The vascular system is a prerequisite for this evolutionary event, providing upright stature and communication for sink demand–source capacity and facilitating the development of plants and colonization over a wide range of environmental habitats. Various hormonal and non-hormonal regulatory networks have been identified and reviewed as key processes for vascular formation; however, how these factors have evolutionarily emerged and interconnected to trigger the emergence of the vascular system still remains elusive. Here, to understand the intricacy of cross-talks among these factors, we highlight how core hormonal signaling and transcriptional networks are coalesced into the appearance of vascular plants during evolution.

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Introduction

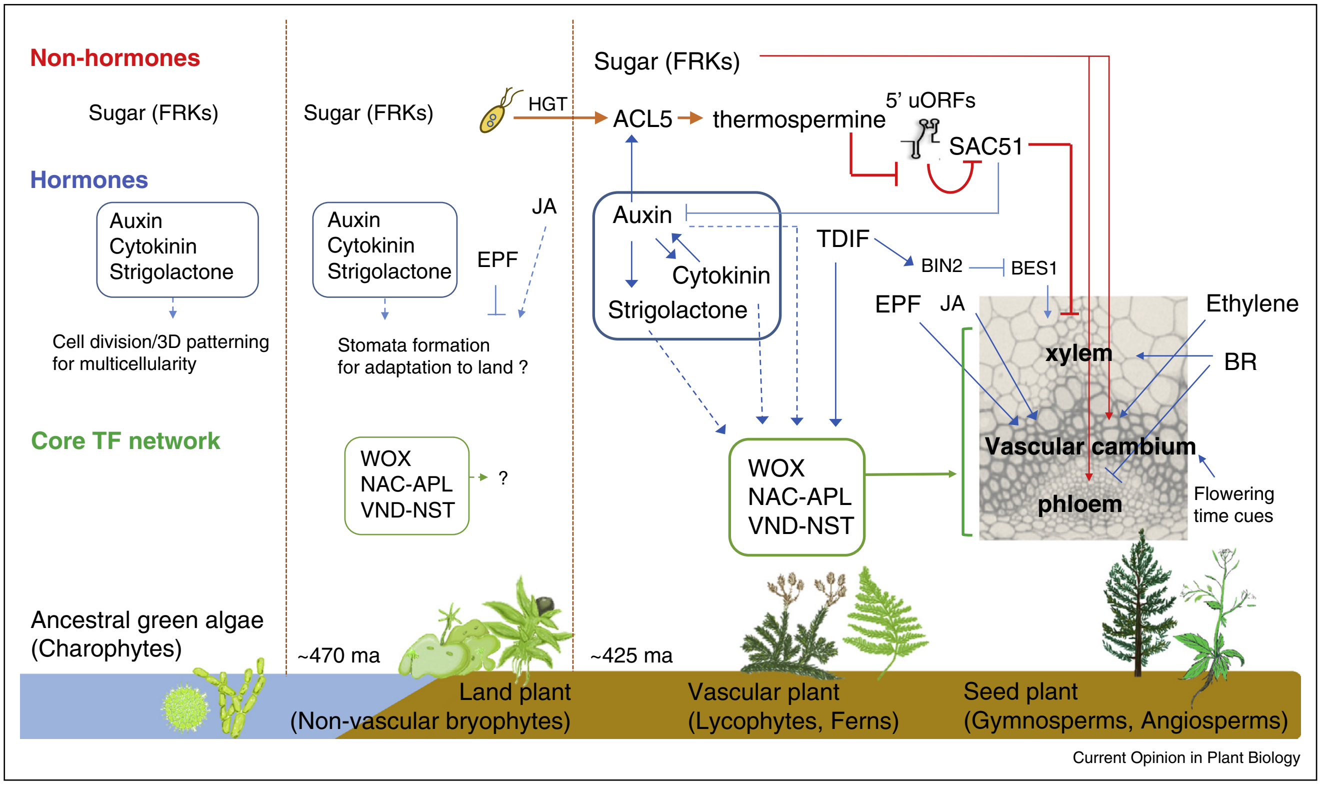
Unlike unicellular organisms that can directly take up nutrients through the membrane, multicellular organisms have developed circulating systems, termed vascular tissues, for delivering essential resources to each cell. Land plants have evolved a specialized unique vascular system consisting of the phloem, meristematic (pro)cambium, and xylem, in which the phloem and xylem act as specialized conduits, transporting photosynthates, mobile signaling molecules, water, and soluble minerals in a highly organized manner [1]. Not surprisingly, as the adaptation of land plants to the ever-changing environmental conditions has heavily relied on the vascular system, the formation and development of vascular bundles are under the tight control of genetic circuits at multiple levels [2•]. During recent years, significant progress has been made in elucidating the molecular mechanisms regulating vascular development, including the isolation of key regulators of vascular tissues such as the WUSCHEL-LIKE HOMEOBOX (WOX) in cambium maintenance, the ALTERED PHLOEM DEVELOPMENT (APL)-NAC DOMAIN-CONTAINING PROTEIN (NAC) module in phloem differentiation, and the VASCULAR-RELATED NAC-DOMAIN PROTEIN (VND)-NAC SECONDARY WALL THICKENING-PROMOTING FACTOR (NST) module in xylem maturation. For more detailed information on vascular development, we refer readers to other recent reviews [3,4,5•].

As the vascular system could have emerged because of selection pressure experienced by land plants to survive and develop in terrestrial conditions, genetic changes to trigger the formation of vascular bundles should exist. However, regardless of intensive genetic screenings, the developmental cues and genetic programs that directly and/or specifically regulate the emergence of vascular bundles during evolution, particularly during the late Silurian (ca. 425 million years ago), remain unknown. In the present review, to gain some insights into the genetic switches responsible for the formation of vascular bundles during evolution, we focus on new genetic roles of old players, including hormonal and non-hormonal cues, for example, sink demand–source capacity and nutrient homeostasis, and the manners in which these factors coordinate during the emergence of vascular bundles in land plants.

Old player 1: the role of hormones in the regulation of vascular development

Several plant hormones such as auxin, cytokinin, and strigolactone originated in charophytes [6••] and possibly functioned as ancient regulators during the adaptation of land plants to terrestrial environment followed by the formation of vascular bundles in early vascular plants [7,8] (Figure 1). Besides their important roles in most aspects of plant development [9,10], auxin, cytokinin, and strigolactone have been shown to be key positive regulators of cambium activity. Small changes in the biosynthesis, transportation, and signaling of these hormones lead to impaired cambium activity, and consequently, defective vascular development. Auxin accumulation is restricted to the cambial region and is highly correlated with cambium activity during the initiation of secondary growth [11,12]. In the *Arabidopsis* inflorescence stem, mutations in auxin transporter PINs (PIN-FORMEDs) have been

Figure 1



A schematic representation of the regulatory networks during the evolution of the plant vascular system. Non-hormonal, hormonal, and core transcriptional factor (TF) networks regulating vascular formation are highlighted as red, blue, and green lines, respectively. Note that the horizontal gene transfer (HGT) event of ACAULIS5 (ACL5) from prokaryotes to plants during the divergence of vascular plants is implicated in multiple levels of regulation among non-hormonal and hormonal interactions for the emergence of the plant vasculature, particularly xylem formation. The developmental roles of ancient hormones and core transcriptional networks in the ancestral green algae and non-vascular land plants as well as the interconnection of these factors in the emergence of the vascular system during the evolution of vascular plants remain unknown. Solid lines indicate demonstrated interactions, and dotted lines represent possible links among the networks.

shown to cause the suppression of auxin transport, resulting in severe defects in cambium activity [13]. Nevertheless, despite the well-established role of auxin signaling as well as the isolation of key regulators of auxin signaling in cambium activity [3,4,5•], how downstream auxin-mediated transcriptional reprogramming regulates cambium activity remains unclear. Cytokinin biosynthetic and signaling mutants have also been shown to have severe defects in cambium activity, accompanied by reduced thickening of roots and stems [14–16]. MORE AXILLARY BRANCH (MAX) proteins are involved in strigolactone biosynthesis and signaling. The *max* mutants characterized by strigolactone deficiency exhibit a decreased production of cambium-initiated secondary growth in *Arabidopsis* [17]. These observations highlight the importance of hormone homeostasis in plant vascular development.

Jasmonic acid (JA) arose in the liverwort *Marchantia polymorpha*, the last common ancestor of land plants, whereas ethylene and brassinosteroids (BRs) emerged more recently within the plant kingdom during the evolution of angiosperms [6••]. Although both JA and ethylene play positive roles in the regulation of cambium activity [18,19], BRs show more diverse functions in vascular development, being positive regulators of xylem differentiation and repressors of phloem differentiation [20] (Figure 1). Exogenous JA application has been shown to enhance cambium activity during secondary growth in *Arabidopsis*, and the components of JA signaling, including CORONATINE INSENSITIVE 1 (COI1), and JASMONATE ZIM-DOMAIN (JAZ) proteins, are cambium regulators [18]. Mutations in positive regulators of ethylene responses, including ETHYLENE RESPONSE FACTOR (ERF) transcriptional factors, result in significant reduction of the number of cells per vascular bundle, indicating decreased cambium activity. On the other hand, ethylene overproducing mutants show larger vascular bundles with enhanced cambial cell division [19]. Phenotypic analyses of BR signaling as well as biosynthesis-deficient and BR-overproducing mutants have revealed the functions of BRs as modulators of vascular