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The logic of plant vascular patterning. Polarity, continuity and plasticity in the formation of the veins and of their networks

Enrico Scarpella

The problem of long-distance transport is solved in many multicellular organisms by tissue networks such as the vascular networks of plants. Because tissue networks transport from one tissue area to another, they are polar and continuous; most of them, including plant vascular networks, are also plastic. Surprisingly, the formation of tissue networks is in most cases just as polar, continuous and plastic. Available evidence suggests that the polarity, continuity and plasticity of plant vascular networks and their formation could be accounted for by a patterning process that combines: (i) excess of developmental alternatives competing for a limiting cell-polarizing signal; (ii) positive feedback between cell polarization and continuous, cell-to-cell transport of the cell-polarizing signal; and (iii) gradual restriction of differentiation that increasingly removes the cell-polarizing signal.

Address
Department of Biological Sciences, University of Alberta, CW-405
Biological Sciences Building, Edmonton, AB T6G 2E9, Canada

Corresponding author: Scarpella, Enrico (enrico.scarpella@ualberta.ca)

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Plant vein networks and their logic

In higher plants, sugars need to be transported from shoot organs such as branches and leaves, where they are produced, to the roots [1]. Furthermore, water and minerals need to be transported from the roots, where they are absorbed, to the shoot organs. This problem of long-distance transport is solved by a network of vascular strands: bundles of vascular cell files, to which, for brevity and simplicity, I will refer as 'veins' (Figure 1).

The specialized transport function of the veins and of their networks is reflected in their properties (Figure 1). First, veins connect primarily shoot organs with roots [2], and are thus unequal at their ends: one end connects to shoot tissues, the other to root tissues. Therefore, veins are polar [3]. Second, veins contact other veins at least at one of their two ends to give rise to continuous networks [4]. Third, details of the veins and of their networks are innately variable: the number of veins; their shape, length and location; whether they contact other veins at both their ends or only one of them, and if so which one [5,6••,7,8] (Figure 1). Most important, this variability is a form of plasticity in no relation to environmental heterogeneity [9,10].

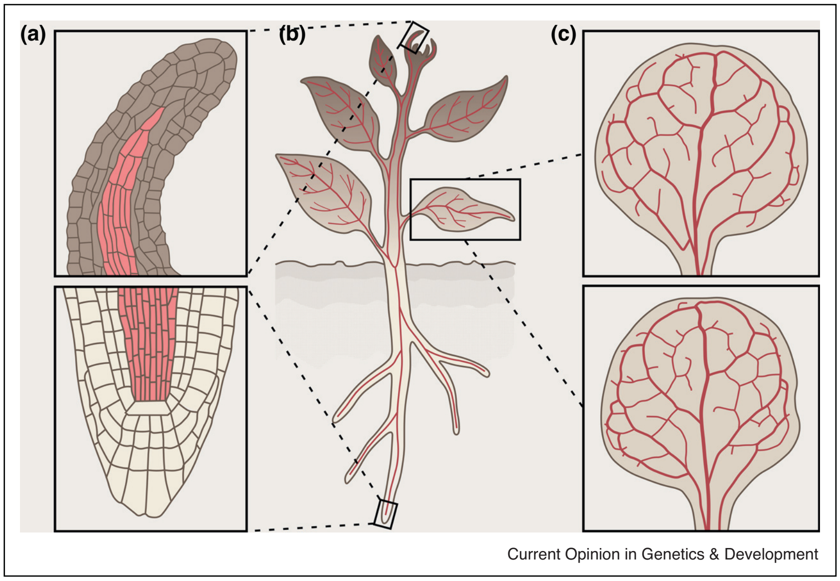
Polarity, continuity and plasticity are not only properties of the mature veins and of their networks but organizing principles of their formation. Here I will focus on these principles. I will emphasize the 'syntax', as it were, of the patterning process, rather than its 'semantics'. This latter has been reviewed recently and comprehensively (*e.g.*, [11–14,15•,16•,17•,18•,19•,20•]).

The formation of the first vascular cells

Most of the body of a seedling can be thought of as a cylinder with a vein in its center (Figure 2a). The formation of this cylinder in the Arabidopsis globular embryo is associated with the formation of the first vascular cells, which originate from the asymmetric division of the lower inner cells of the dermatogen-stage embryo [21••,22,23,24••,25] (Figure 2b). These first vascular cells make polar contacts: their apical end contacts the upper inner cells, and their basal end contacts the uppermost cell of the suspensor. Furthermore, the localization of the Arabidopsis plasma-membrane protein PIN-FORMED1 (PIN1), which controls the polarity of the transport of the plant hormone auxin [26] (Figure 3), is distinctively polarized in these first vascular cells [27–31,32••] (Figure 2b).

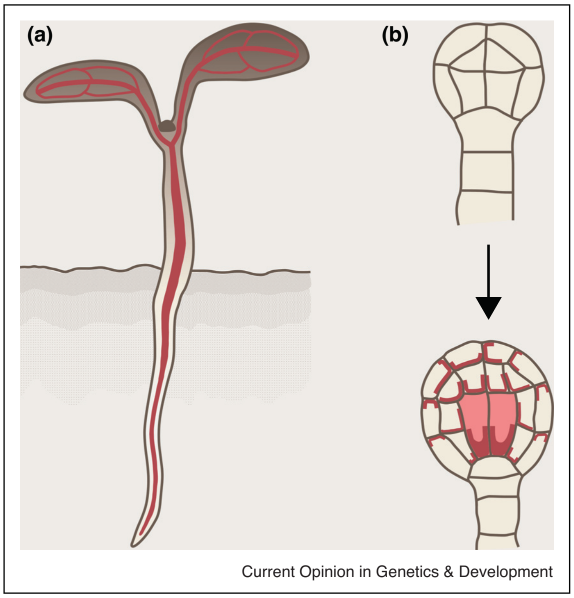
Available evidence suggests that the formation of the seedling cylinder and the vein in its center depend on polar auxin transport and signaling. Embryogenesis in the presence of auxin transport inhibitors occasionally leads to nearly spherical, seemingly nonpolar, embryos and seedlings [33,34]. Similar defects seem to characterize the most severe phenotype classes of *pin* multiple mutants [35] and of mutants in the Arabidopsis gene *EMBRYO DEFECTIVE30/GNOM* (*GN* hereafter) [36–38], which is required to coordinate the cellular localization of PIN proteins across tissues [27,39,40].

Figure 1



The logic of plant vein networks. **(a)** Continuous files of vascular cells (light-red fill) are bundled into veins. **(b)** Veins (dark-red lines) contact shoot tissues (dark-brown fill) at one end and root tissues (light-brown fill) at the other, and are thus polar. **(c)** Though veins reproducibly supply all areas of the plant, their details are innately variable, as shown by the vein networks of two first-leaves of Arabidopsis grown in the same conditions (drawn from Ref. [120]).

Figure 2



The formation of the first vascular cells. **(a)** Most of the seedling body is a cylinder with a vein in its center (dark-red line). **(b)** The vein in the center of the seedling cylinder originates from the division of the vascular cells (light-red fill) of the globular embryo (bottom); PIN1 (dark red) localization is polarized in such vascular cells, which originate from the asymmetric division of the lower inner cells of the dermatogen-stage embryo (top).

However, only a small fraction of *pin* and *gn* embryos develops into nearly spherical seedlings; most of them develop into seedlings in which the veined cylinder is replaced by a veinless cone [35,36]. This defect also characterizes embryos developed in the presence of auxin antagonists and mutants in auxin production, perception or response [34,41–49,50••,51]. Among these mutants, defects are most severe in mutants lacking the function of the Arabidopsis gene *MONOPTEROS/AUXIN RESPONSE FACTOR5* (*MP* hereafter), which encodes a transcription factor that regulates auxin-responsive gene expression [41,52–55], and in mutants with a stabilized variant of the otherwise short-lived MP-inhibitor INDOLE-3-ACETIC ACID12/BODENLOS [42,56–58].

The failure of these mutants to form the first vascular cells seems to derive from the inability of the lower inner cells of the dermatogen-stage embryo to divide asymmetrically, suggesting that polar auxin transport and signaling promote such asymmetric cell divisions [24••,56]. However, this ability of auxin seems to be dispensable to the formation of veins that occurs in various tissues in response to auxin application [59,60]. Therefore, it seems that the vascular-differentiation-promoting influence of auxin does not necessarily depend on its cell-division-orienting activity.

The plasticity of vein formation

Application of auxin to various tissues leads to the formation of continuous files of vascular cells that connect the