

Canalization: what the flux?

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Polarized transport of the hormone auxin plays crucial roles in many processes in plant development. A self-organizing pattern of auxin transport – canalization – is thought to be responsible for vascular patterning and shoot branching regulation in flowering plants. Mathematical modeling has demonstrated that membrane localization of PIN-FORMED (PIN)-family auxin efflux carriers in proportion to net auxin flux can plausibly explain canalization and possibly other auxin transport phenomena. Other plausible models have also been proposed, and there has recently been much interest in producing a unified model of all auxin transport phenomena. However, it is our opinion that lacunae in our understanding of auxin transport biology are now limiting progress in developing the next generation of models. Here we examine several key areas where significant experimental advances are necessary to address both biological and theoretical aspects of auxin transport, including the possibility of a unified transport model.

Auxin and self-organization in plant development

The hormone auxin (see [Glossary](#)) regulates almost every aspect of plant development, and the directional movement of auxin by a specialized transport system (polar auxin transport, PAT) is crucial for many of these processes ([Box 1](#), [Figure 1A](#)) [1]. In simple cases, fine-scale redistribution of auxin allows for differential responses in different cells, driving patterning and specification events. However, in many cases patterns are generated not simply by auxin redistribution but emerge as a property of the system of feedback between the tissue, auxin, and auxin transport. It is widely supposed that these developmental systems, and the auxin transport patterns that drive them, are self-organizing – that is, little or no pre-pattern is needed [2]. Understanding these apparently self-organising phenomena has long been an area of interest, as exemplified by research on phyllotaxis – the pattern of leaf initiation at the shoot meristem ([Figure 1B](#)) – and the vascular patterns of leaves ([Figure 1C](#)).

Because of their self-organizing properties, intuitive understanding of these systems is difficult and there has therefore been considerable interest in mathematically modeling these phenomena [3]. Vascular patterning and

phyllotaxis have primarily been simulated using two fundamentally different (but non-exclusive) auxin transport heuristics, often respectively referred to as ‘with-the-flux’ (WTF) and ‘up-the-gradient’ (UTG) ([Box 2](#)). Although these models have been immensely useful in demonstrating the plausibility of self-organizing transport as a developmental mechanism, neither type of model is explicit about their biological basis, and they include parameters that are not based in current mechanistic understanding, such as assessment of auxin concentration in neighboring cells. Furthermore, it is probable that neither heuristic is inherently capable of capturing the full range of self-organizing auxin transport [3]. To understand better the role of self-organizing auxin transport in plant development, a new generation of models that are more deeply rooted in a mechanistic understanding of auxin biology is needed. However, our understanding of the biology of canalization and related phenomena has been somewhat outstripped by theoretical work on these problems, and now represents a limiting factor for modeling. The purpose of this article is thus not to propose a next-generation model but to examine the areas in which we need to improve our understanding of auxin transport and discuss how current models can be used to prioritize these experiments. We primarily discuss WTF models, particularly in the context of the canalization hypothesis, vascular patterning, and shoot branching. There has recently been considerable interest in attempting to unify models of auxin transport, and we also assess prospects for achieving this goal.

The canalization hypothesis of vascular patterning

Vascular patterning in plants is ‘complex but orderly’ [4] – it is not hardwired but clearly proceeds according to firm principles such that the same general vascular topology is reproduced in almost every individual in a species ([Figure 1C](#)). Local auxin application induces vascular differentiation in plant tissue, but in narrow strands running away from the application site, rather than in wide fields of cells [5]. These observations led to the singular and pioneering contributions of Tsvi Sachs, whose elegant experiments are still central to the field [4,6–8]. Sachs proposed that as auxin flows through tissues it upregulates and polarizes its own transport, which gradually becomes channeled – or ‘canalized’ – into files of cells with very high auxin flux away from auxin sources ([Figure 1D](#)); these cell files can then differentiate to form vasculature ([Figure 2](#)) [7,8]. Sachs also demonstrated that new vasculature usually develops towards and unites with existing vasculature strands, leading to a connected vascular network ([Figure 2](#)) [4,7,8]. However, he also demonstrated that existing vasculature could be ‘hyper-canalized’ by the addition of

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Glossary

Angiosperms: flowering plants. By far the largest major grouping of plants and also the most recently evolved. Includes almost all crop species and model species such as *Arabidopsis thaliana*.

Apoplast: the space between plant cells, occupied by thick cellulosic walls (Figure 1A). There is a significant pH difference between the apoplast (pH 5.5) and cytoplasm (pH 7), and this directly affects auxin transport in accordance with the chemiosmotic hypothesis.

***Arabidopsis thaliana*:** a principal plant model species, particularly for molecular genetic studies, due to its small size, small genome, and short life-cycle. Its small size, however, means that it is not ideally suited to canalization research.

Auxin, auxin transport: auxin (indole-3-acetic acid, IAA) is a low molecular weight, long-distance signal with many functions in plant development. Specific, polar auxin transport (PAT) through tissues seems to be an ancient characteristic of land plants.

Canalization: an apparently self-organizing pattern of auxin transport in which an initially broad domain of auxin-transporting cells is reduced to a narrow ‘canal’. This is thought to occur by auxin upregulating and polarizing its own transport.

Charophyte algae: a group of green algae that constitute the sister taxon of land plants.

Chemiosmotic hypothesis: see Box 1.

Gymnosperms: a diverse group of plants, including conifers, that produce seeds but not flowers. Together with angiosperms they make up the seed-plant (spermatophyte) clade.

Lycophytes: an ancient group of vascular plants; sister taxon to the clade containing ferns and seed plants.

Maximization: an apparently self-organizing pattern of auxin transport in which auxin is transported towards cells containing higher concentrations of auxin, leading to the formation of an auxin ‘maximum’.

Meristem: a specialized region of cell division in plants. Shoot meristems in angiosperms and gymnosperms combine cell division with the production of new organs, either leaves or reproductive structures. Shoot meristems in other plants are generally simpler in structure and contain far fewer cells. Root meristems are only present in vascular plants and do not directly produce new lateral organs.

Phyllotaxis: an apparently self-organizing developmental pattern describing the position of organs (e.g., leaves) along and around the stem. Different phyllotactic patterns occur in different species. Phyllotaxis in angiosperms results primarily from the positioning of new organ primordia on the flanks of the multicellular shoot meristem, and is established by maximization-like patterns of auxin transport in the meristem.

PIN auxin efflux carriers (‘PINs’): a family of proteins that are generally accepted to be auxin efflux carriers. Canonical PIN proteins have plasma membrane localizations, often polarized, and are thought to be the principal determinants of the direction of auxin efflux, in line with the chemiosmotic hypothesis. Named after a founding member, PIN-FORMED1 (PIN1), in turn named for its mutant phenotype involving impaired organ initiation at the shoot meristem – a result of aberrant maximization.

PINOID-family kinases: a small family of serine/threonine kinases that phosphorylate the intracellular loop of canonical PIN proteins, thereby controlling their localization. Named after the founding member, PINOID, in turn named for the resemblance of its mutant phenotype to *pin1*.

Super-linear: a mathematical relationship in which one variable is influenced by another with a greater than linear effect; examples include quadratic ($y = ax^2$), cubic ($y = ax^3$), and exponential ($y = a^x$) functions.

Up-the-gradient (UTG): a modeling heuristic widely used to simulate maximization-like patterns of auxin transport (Box 2), in which PIN proteins are allocated to the plasma membrane in proportion to the concentration of auxin in cells neighboring that membrane.

Vascular patterning: an apparently self-organizing developmental phenomenon in which the position of future veins is established by canalization-like patterns of polar auxin transport through a tissue.

Vascular plants: the plant clade containing angiosperms, gymnosperms, ferns, and lycophytes. Defined by the presence of a differentiated vascular network. Non-vascular plants such as mosses lack specialized tissues for water transport and are limited in their size as a result.

Vasculature/veins: the vascular network in plants plays analogous roles to the vascular system in animals. It consists of two parallel systems, xylem (primarily water-conducting) and phloem (primarily sugar-conducting), that generally develop in association with each other.

With-the-flux (WTF): a modeling heuristic widely used to simulate canalization-like patterns of auxin transport (Box 2) in which PIN proteins are allocated to the plasma membrane in proportion to the net flux of auxin through that membrane.

auxin, in which case developing vasculature could not ‘find’ and unite with it (Figure 2) [7].

The work of Sachs pre-dated the advent of molecular genetics, and he therefore needed to infer upstream events based largely on terminal vascular differentiation patterns.

Remarkably, recent investigations have supported his hypotheses at a molecular level – including the central canalization concept that, from an initially broad domain of cells with low auxin flux, a subset of cells become progressively more polarized and competent to transport auxin – and have shown that canalization is an important component of vascular patterning [9–11]. It should be emphasized that, although some auxin flows do undoubtedly canalize, not all auxin transport phenomena involve canalization. For instance, initiation of leaf primordia in angiosperm shoot meristems (Figure 1C) requires formation of an auxin maximum by a focused pattern of transport (‘maximization’) (Figure 1D) [12]. Canalization has generally been explored through WTF models (Box 2) which can accurately simulate patterns of auxin transport in a number of developmental processes, including vascular formation in stems and leaves [13–15]. Canalization of auxin transport has also been recently modeled as an explanation for the inhibition of bud outgrowth by actively growing shoots, a scenario in which the development of vasculature is not directly considered, although it is an important additional outcome of the bud activation process [16]. Auxin transport canalization thus has the potential to explain multiple developmental phenomena in plants.

What is the ‘flux’?

All current models of canalization are based on a large corpus of research into polar auxin transport, and in particular the behavior of PIN-family auxin efflux carriers (Box 1). Examination of phyllotaxis and vein formation has shown very distinctive patterns of PIN protein localization consistent with canalization and maximization [9,12,17]. Almost all modern models of auxin transport therefore explicitly simulate membrane-localized PIN proteins that directly influence the amount and direction of auxin transport. The main difference between the WTF and UTG models, based on the experimental observations of PIN protein localization in different scenarios, relates to the rules for allocating PIN proteins to membranes (Box 2). In WTF models PIN proteins are allocated to each membrane in a cell in proportion to ‘flux’, the net quantity of auxin that exits the cell across that membrane. Net flux efficiently couples cells together (because high net flux from cell $i \rightarrow j$ tends to prevent high flux from $j \rightarrow i$), allowing cells to couple to larger-scale patterns of flux and speeding the emergence of global WTF patterns in the overall direction $i \rightarrow j$ (Box 2). Although mathematically this is a very neat solution, as a concept it is likely to be unrealistic because it requires a cell to calculate the net exchange of auxin across its membranes (including passive uptake). There is no known biological mechanism that achieves this, which is a common criticism of flux-based models [18]. Nevertheless, it is clear that cells in real systems do canalize auxin transport, and do so by allocating PIN proteins apparently in proportion to net auxin flux. It is thus the absolute crux of canalization research to establish how cells are able to localize PIN proteins in relation to larger-scale patterns in a self-organizing manner.

The most plausible explanation for the apparent ability of cells to calculate net flux is that cells measure one or more other variables, the combined effect of which is

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