Plant morphogenesis: long-distance coordination and local patterning

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The overall morphology of a plant is largely determined by developmental decisions taken within or near the terminally positioned apical meristems of shoots and roots. The spatial separation of these developmental centers emphasizes the need for long-distance signaling. The same signaling events may simultaneously coordinate differentiation within meristems and in the connecting vascular tissues. Recent genetic and molecular analyses not only confirm the proposed role of auxin as a coordinating signal across the plant, but also implicate auxin as a patterning signal in embryo and meristem organization.

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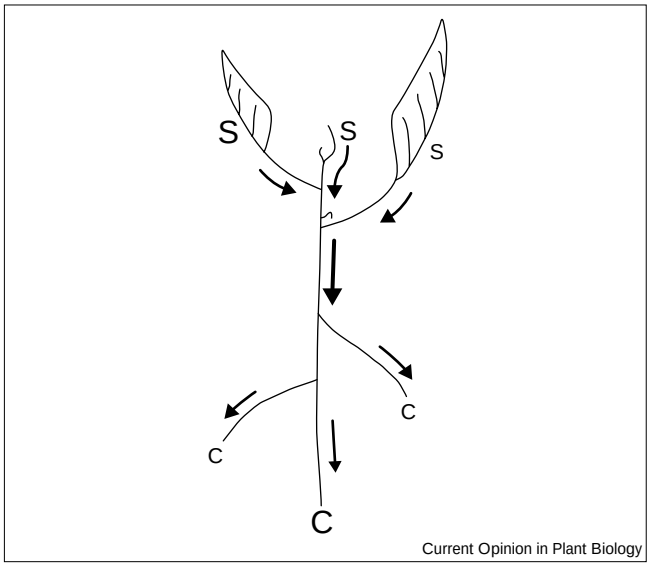
Abbreviations

AAO	ascorbate oxidase
AXR6	*AUXIN RESISTANT 6*
BDL	*BODENLOS*
IAA	indole acetic acid
mp	*monopteros*
PIN1	*PIN FORMED 1*
QC	quiescent center

Figure 1



Auxin as a signal integrating developmental processes throughout the plant. The main elements of the signal are auxin synthesis (S), transport (arrows) and catabolism (C). The apparent levels of these activities throughout the plant are indicated by the sizes of letters or arrows. All of these elements can potentially be changed by mutation or other perturbations. Auxin sources in the shoot generate correlative information, which orients vascular differentiation and induces root initiation.

Introduction

Auxin has been implicated in a bewildering array of developmental processes. A partial list includes responses to the environmental cues of light and gravity, the control of dominance relations among shoot apices, the initiation of new root meristems, the organization of embryos, the patterned differentiation of vascular tissues and the differentiation of single cells to become tracheary elements [1–7]. These phenomena are not only varied, they also occur at different levels of organization from the whole plant to the single cell [8•].

Recent molecular genetic work appears to add to the confusion by implicating auxin directly in the patterning processes in embryos and meristems. In this review, we make suggestions for the integration of long-distance coordinating auxin functions with local-patterning functions in embryos and meristems. Further, we attempt to show that these suggestions offer some insights concerning both the most recent contributions to auxin research and future possibilities.

Coordination of morphogenesis throughout the plant

Auxin serves as a major integrator of developmental processes at many levels and throughout the plant [3,6,9]. More specifically, it is a signal that coordinates the development of various plant tissues with the state and size of the shoot tissues that are morphologically above them (Figure 1). Auxin coordinates the growth of new leaves with the initiation of new roots. At the same time, it determines both the differentiation of and the relations among cells of the vascular contacts between these new organs. The formation of auxin signifies not only the initiation of new leaves, but also the position and size of mature ones. Moreover, the correlative effects of leaves that are in light on developmental events throughout the plant are greater than of those in shade, indicating that long-distance signals continuously monitor the state of the shoot in its environmental context [10].

Is it possible that a single type of molecule — indole acetic acid (IAA), the major type of auxin in higher plants — has instructive functions in such a variety of developmental processes or is auxin's role overestimated? Two explanations for multiple auxin functions seem plausible. Auxin could either act as a versatile intercellular messenger in a variety of otherwise unrelated cell interactions or confer fundamental types of patterning information, such as polarity and axial differentiation, which in turn is essential in a multitude of local cell-patterning processes. Genetic

analysis seems to provide examples to support both explanations. First, candidate genes in auxin signal transduction have turned out to be members of large gene families, which are sufficiently complex to account for the parallel relay of numerous independent messages [11,12]. Mutations in these gene families have been isolated [5,13,14•,15,16•,17•], and ongoing genetic analyses can be expected to generate a floor plan of interacting pathways in the near future. Second, highly related complex phenotypes, such as those of embryo axis formation mutants (see below), indicate a defect in a fundamental underlying auxin-dependent process, cell axis alignment, which impinges on many aspects of plant morphology.

Although attention usually focuses on auxin perception, it should be remembered that perturbations involving auxin, whether caused by mutation or other means, may result from interference with auxin signaling at four levels. First, there could be perturbations of auxin synthesis, and of the relations between auxin synthesis and the age of the tissue or environmental conditions. Second, the essential transport of auxin through the plant [18,19] might be affected, such transport could be critical for localizing auxin in responding tissues [20]. Third, changes within cells might affect the activity of auxin on receptors, and fourth, the consumption or metabolism of auxin, which is essential for its movement through the plant and its action as an integrating signal, might be perturbed in some way. This consumption can be expected to occur in the roots, where auxin accumulates as a result of polar transport, and may even be localized within specific parts of root meristems [21].

In the following sections, we discuss recent evidence for auxin-mediated patterning in embryos and meristems from the perspective that separated local-patterning functions and auxin-mediated shoot–root signaling form an integrated mechanism, which continuously coordinates morphogenesis throughout the plant.

Embryo axis formation

Recently identified mutations in two genes, *AUXIN RESISTANT 6* (*AXR6*) [22•] and *BODENLOS* (*BDL*) [23•], result in phenotypically similar rootless seedlings with reduced vascular systems and occasionally fused cotyledons. In the embryos of mutants affected in these genes, early cell divisions are abnormally oriented and do not establish cell files along the apical–basal axis. By all these criteria, both mutants resemble the previously identified *monopteros* (*mp*) mutants, and the *MP* gene has been implicated in the relay of an apical–basal auxin signal and encodes an 'Auxin Response' transcription factor [5,24]. One may speculate, therefore, that all three genes function in auxin signal transduction to promote the alignment of cell differentiation with the apical–basal orientation of auxin flow. Consistent with this interpretation, certain responses to auxin application, such as hypocotyl swelling and callus formation, were reduced in *bdl* mutants, whereas dominant *axr6* alleles were shown to confer reduced apical dominance, reduced lateral root formation and auxin-insensitive root elongation.

The most conspicuous defect in the *mp*, *bdl*, *axr6* class of mutants is their failure to produce a primary root. This local focus, however, is not absolute: in *mp ; bdl* double mutants, the apical pattern of the embryo is no longer organized, suggesting that all types of directional growth eventually depend on auxin signaling [23•]. Interestingly, mutations in a single *Arabidopsis* gene, *EMB30/GNOM*, can abolish cell polarity in the entire embryo, and null-mutations in another gene, *PIN FORMED 1* (*PIN1*), result in related but far less severe distortions of embryo symmetry [25••,26]. Both gene functions seem to be required for proper auxin transport. The PIN1 product is the best characterized member of a family of presumptive auxin efflux carrier proteins [26], whereas *EMB30/GNOM* encodes a guanosine exchange factor acting on small G-proteins in vesicle transport [25••]. Mutations in *EMB30/GNOM* seem to interfere with vesicle transport, which is required for the coordinated polar localization of the PIN1 product, and they may, therefore, also affect the localization of other auxin efflux proteins. According to this interpretation of the *EMB30/GNOM* and *PIN1* functions, auxin transport and coordinated localization of auxin efflux proteins are prerequisites for directional growth in morphogenesis anywhere in the plant.

Root meristem formation and maintenance

The promoting influence of auxin on root meristem formation is experimentally well established, and the rootless embryos of *axr6*, *bdl* and *mp* mutants suggest that auxin signals are also required for the initiation of the primary root early in embryogenesis. A recent study seems to provide not only a molecular explanation for the auxin-dependence of root meristem initiation, but also evidence for a role of auxin as a positional signal in the cell-patterning process within the root meristem [27••]. The experimental strategy for this study is based on the precise localization of an auxin response, which enabled the authors to correlate its position with those of cell differentiation events in the meristem. The expression of a reporter gene under the control of a synthetic 'Auxin Response' element genuinely reflected auxin distribution when roots were exposed to external auxin, and could therefore be expected to monitor the distribution of 'perceived' auxin in the growing root.

A sharp-bordered local auxin maximum (i.e. auxin peak) just distal to the quiescent center (QC) was observed in the undisturbed *Arabidopsis* root meristem. Most importantly, any shift in the localization of this peak, whether caused by genetic or experimental interference with auxin transport, was associated with shifts in the pattern of distal cell fates in the root meristem. The most dramatic shift was observed upon long-term inhibition of auxin transport by the auxin efflux inhibitor NPA (N-[1-naphthyl]phtalamic acid). After several weeks, a centrally positioned

auxin peak was flanked on either side by inversely polarized root segments. The fact that manipulations of the position of the auxin peak by various methods were associated with corresponding changes in the cellular pattern suggests that auxin distribution has an instrumental role in root meristem patterning. In normal plant development, the formation of a local auxin peak would probably depend on shoot-derived auxin. The peak and its shoot-dependent positioning would therefore reflect both the coordinating and the local-patterning functions of auxin in root meristem formation. In future studies, auxin response markers will be well suited to trace the origin of auxin signals and, hence, to test this interpretation.

How could a peak of local auxin concentration remain stable during the continuous proliferation of cells in the active root meristem? A permanent auxin peak in the center of the root meristem would obviously require the dynamically controlled expression of an auxin-inactivating function at the distal end of the stele, where auxin would be expected to enter the meristem. A recent study by Kerk *et al.* [28•] illustrates, how such a feedback mechanism could operate. The results extend earlier observations that had shown that ascorbic acid is required for the G_1 to S transition in the cell cycle, and that the ascorbic acid catabolizing enzyme ascorbate oxidase (AAO), as well as auxin, is concentrated in the QC of maize root meristems [21]. Therefore, the local upregulation of the AAO gene could account, at least in part, for the reduced cell proliferation within the QC. The AAO gene is auxin inducible and, thus, may be activated in the QC as a result of auxin transport through the stele. The new study demonstrates that the AAO enzyme can oxidatively decarboxylate auxin and the resulting feedback loop could confine enhanced concentrations of both AAO and IAA to the QC [28•]. Although there is no direct evidence that the observed interactions between AAO and IAA are functionally relevant for the stability of the root meristem pattern, they provide a perspective on how biochemical interactions could establish a robust coarse pattern. This pattern could be further refined by other types of cell interaction. In summary, the new results are consistent with a dual function of auxin as a long-range signal promoting root formation and a positional signal within individual root meristems.

Lateral organ formation in the shoot apex

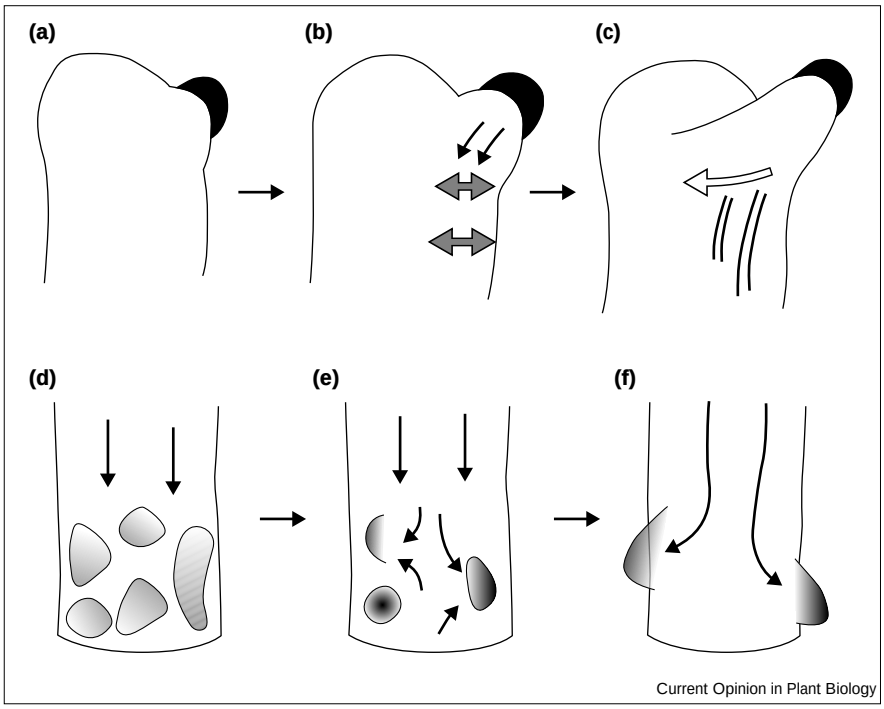
Although the distribution of auxin sources in the shoot apex is still unclear, there is general agreement that young leaf and flower primordia are important sources of auxin [2,3]. Interestingly, these lateral outgrowths within shoot apical meristems are not formed when auxin transport is impaired, suggesting that auxin transport either towards or away from a primordium is required for its patterned growth. In a recent study, Reinhard *et al.* [29•] demonstrated that lateral organ formation in meristems in which auxin transport is inhibited can be restored by local application of auxin. Minute amounts of IAA were applied onto the surfaces of auxin-transport-inhibited vegetative meristems of tomato and to inflorescence meristems of the *Arabidopsis* reduced-auxin-transport mutant, *pin1*. In both systems, lateral organs (i.e. leaves or flowers, respectively) developed at the sites of auxin application. These results are consistent with the action of auxin as a positional signal that determines the site of directional growth in a shoot meristem. Furthermore, the amount of auxin applied to a given site determined the circumferential size of the primordium (Figure 2). As in the embryo and the root meristem, auxin positional signaling in the shoot meristem seems to be integrated into a larger patterning context. IAA application can induce lateral organ formation only at certain distances from the meristem tip, suggesting that cells pass through a transient phase of response competence as they are displaced from the tip.

The new findings are consistent with the previously observed formation of (less organized) lateral structures after local auxin application to pea meristems [30]. The local growth responses suggest that auxin peaks are sufficient to induce lateral outgrowth in competent zones of shoot meristems and that the amount of auxin determines the circumferential size of the new primordium. In extreme cases, a large amount of auxin can induce the formation of an oversized, collar-shaped primordium that encloses the apex. This observation raises the question of what delimits the size of leaf primordia in normal development, because young leaf primordia are, themselves, important auxin sources. The auxin production of leaf primordia should create a growth-enhancing feedback loop, unless a coupled counteracting mechanism removes or inactivates auxin. Auxin removal could occur through the associated formation of highly auxin-conductive provascular cells beneath the emerging primordium (Figure 2). This mechanism would be consistent with the auxin-mediated induction of new vascular strands by young organ primordia [6,9]. It could also account for the control of lateral organ spacing along the circumference of a shoot meristem (as discussed in detail in [6]).

Auxin as a coordinating and patterning signal

The work reviewed above shows that the analysis of auxin's developmental roles continues at an increasing pace. The phenotypes of a number of auxin response mutants suggest that they are caused by mutations that influence 'master processes' of cellular change. An example of such a master process is the specification of cell orientation (i.e. polarity), which appears to be a basic process that precedes a variety of more specific differentiation events [6,15]. The recent results summarized above confirm that auxin has a major role in determining relations not only among the various organs of the plant but also within developing tissues and, thus, in the patterning of cellular growth and differentiation. These observations should be taken together with the known facts that auxin alone, with no added signals, can induce the organized differentiation of entire complex vascular strands and entire root apices [9].

Figure 2



Model integrating local patterning in shoots and roots with long-range auxin signals. Note that the model stresses the importance of feedback relations between the supply of auxin and cellular responses. (a–c) Auxin plays a major role in leaf initiation and apical organization. (a) Local auxin application (as represented by the black area) can induce the formation of a new leaf primordium close to the shoot apex in competent tissue. Such leaf formation can occur in shoot meristems that, prior to the local application of auxin, were leafless as a result of being treated with an auxin transport inhibitor. (b) The growing primordium orients cell development towards itself (as indicated by black arrows). This pattern of cell development is mediated by the supplied auxin and by the auxin formed within the primordium itself. Feedback between auxin synthesis and its removal by the adjoining axial tissues is essential for continued leaf development. The tissues below the leaf respond to auxin by transverse growth (gray arrows), forming the buttress, which supports the leaf. (c) High levels of auxin induce a large buttress and vascular supply (double lines). They also cause the primordium to spread around the apex (open arrow), as do normal leaves. (d–f) Root apices are both induced and organized by a feedback between the effects of auxin and its localized catabolism. (d) Auxin transported along the polarity of a stem cutting accumulates in the basal region. This accumulation induces the first stages of root cell differentiation, including auxin catabolism, in many groups of cells. (e) As differentiation proceeds, the catabolic capacity exceeds auxin availability and continued differentiation, which requires auxin, is focused to distinct regions. These regions compete for the available auxin. (f) Differentiation is restricted to foci, which grow as observable root apices. Relations among the supply of auxin, differentiation, and auxin catabolism may define distinct regions within the developing root apices. Auxin movement into these apices induces and orients their vascular contacts with the rest of the plant.

How can one signal, auxin, specify the orderly and divergent differentiation of cells? One hypothesis goes back to the concept of the 'morphogen': a substance or activity gradient that supplies positional information, which precedes, and is quite separate from, its specific and elaborate interpretation by the cells [31]. The 'morphogen' concept has since been supported, at least as a component of patterning, in several instances in *Drosophila* development [32]. The possibility that auxin could act as a morphogen has been discussed in various contexts, and sharp concentration differences between neighboring cells have been interpreted as supporting evidence [33,34]. The concept of a rigid concentration gradient that is passively perceived by responding cells is, however, difficult to reconcile with common responses to auxin, which are not concentration specific [35]. What are the alternatives? In the specific case of the roots, how could the effects of auxin become focused to specific locations and specific tissues within apices? Figure 2 depicts a possible scenario in which the earliest stages of root initiation appear at random and their restriction to defined developmental centers depends on the early stages of differentiation itself: root apices catabolize auxin and, thus, create sinks for auxin flow. Continued flow should be required for continued root differentiation and for patterned differentiation within the root apex itself. The new roots and root tissues would thus 'compete' as sinks for the available auxin [6]. This competition would prevent the formation of distorted apices or clustered roots, phenomena that are common when excessive exogenous auxin is applied. A similar hypothesis, based on feedback between the effects of auxin and cellular responses, has been proposed to explain the differentiation of vascular strands [6,15]. Furthermore, feedback between auxin flow and distribution has recently been implicated in self-organized root meristem patterning [36•]. The central role of auxin catabolism in this process could integrate root meristem patterning into a plant-wide signaling network.

In general terms, stable distribution patterns of signaling molecules, such as auxin, could be generated by dynamic, interconnected feedback responses in the shoot and root. Such feedback responses could act by amplifying stochastic differences and stabilizing cell-fate decisions [36•]. Instead of rigid 'morphogen' gradients imposed on passively responding cells, there could be patterns of differential auxin synthesis, transport and catabolism. These processes are expressions of differentiation, but they also change auxin distribution and thus feed back on

ongoing differentiation. The critical information could be the duration and intensity of the cellular response itself. Auxin response peaks are built up slowly and could, therefore, be interpreted as the integration of signaling activity over time, reflecting the ultimate, stable outcome of feedback interference. Thus, the suggested causation is not unidirectional, instead, the feedback controls could check and correct development as it occurs. The positions of differentiating zones would emerge from a dynamic cross-talk and, hence, would not be precisely predictable [37]. Feedback regulation of cell responses would also be essential for development to be robust. Intriguingly, the mechanisms underlying embryo, meristem and vascular development are all extremely flexible and can generate a variety of abnormal, yet functional, patterns in response to constraining conditions.

Conclusions

Auxin has long been known to regulate a wide variety of plant responses, but recent molecular genetic findings directly implicate auxin in the organization of cell patterns and in genetically programmed morphogenesis. Closer inspection of these developmental patterning processes shows that they do not seem to be rigidly specified. Rather, they appear to be flexible and to emerge from complex intercellular cross-talk. It is plausible that auxins act as intercellular messengers in patterning processes in embryos, meristems and vascular development, and that auxin-mediated long-distance signaling could simultaneously integrate morphogenesis throughout the plant. In the future, it will be important to understand how a multitude of auxin signals can be communicated, and which other intercellular signaling molecules are involved in the establishment of basic cell patterns in plants.

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