Adventitious Roots and Lateral Roots: Similarities and Differences

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Abstract

In addition to its role in water and nutrient uptake, the root system is fundamentally important because it anchors a plant to its substrate. Although a wide variety of root systems exist across different species, all plants have a primary root (derived from an embryonic radicle) and different types of lateral roots. Adventitious roots, by comparison, display the same functions as lateral roots but develop from aerial tissues. In addition, they not only develop as an adaptive response to various stresses, such as wounding or flooding, but also are a key limiting component of vegetative propagation. Lateral and adventitious roots share key elements of the genetic and hormonal regulatory networks but are subject to different regulatory mechanisms. In this review, we discuss the developmental processes that give rise to lateral and adventitious roots and highlight knowledge acquired over the past few years about the mechanisms that regulate adventitious root formation.

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INTRODUCTION

Roots are present in all vascular plants, although they do not form in primitive vascular plants such as whisk fern (*Psilotum* spp.) and close relatives, in duckweed (*Wolffiella* spp.), or in Spanish moss (*Tillandsia* spp.) and closely related atmospheric epiphytes. Nonvascular plants such as mosses and liverworts develop threadlike rhizoids that can also be found in gametophytes of vascular plants without seeds, such as ferns, horsetails, and club mosses. Rhizoids absorb water and mineral nutrients but completely lack vascular tissues. In fact, roots always have vascular tissues—i.e., xylem and phloem—that are fundamental for their primary functions: to anchor the plant to the soil, absorb water and minerals, and store photoassimilates.

Root Systems Show Variable Morphologies

The radicle is the initial root of a plant that is initiated during embryogenesis and present in the embryo within the seed. The primary root (PR) of a young plant derives from the elongation of the radicle during germination. There are several possible fates for the PR. In gymnosperms and dicotyledons—including annual plants such as *Arabidopsis thaliana* and tomato (*Solanum lycopersicum* L.) and woody perennials like poplar (*Populus* spp.)—the PR commonly grows to become a thick central taproot, which may or may not develop secondary roots called lateral roots (LRs). LRs reiterate the process and develop higher-order LRs. This structural organization is frequently termed a taproot system or allorhizic system (38) (**Figure 1**). Carrot (*Daucus carota*) has an extreme

LR: lateral root

Figure 1

Schematic representation of typical root systems found in most dicotyledons and monocotyledons.
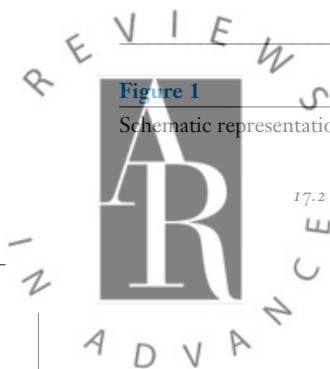
taproot system, with a single thick, central root and very thin LRs (**Figure 1**). In taproot systems, the PR is important during the entire life cycle of the plant.

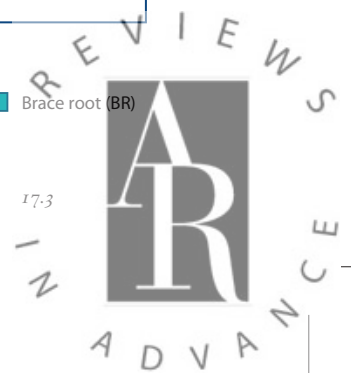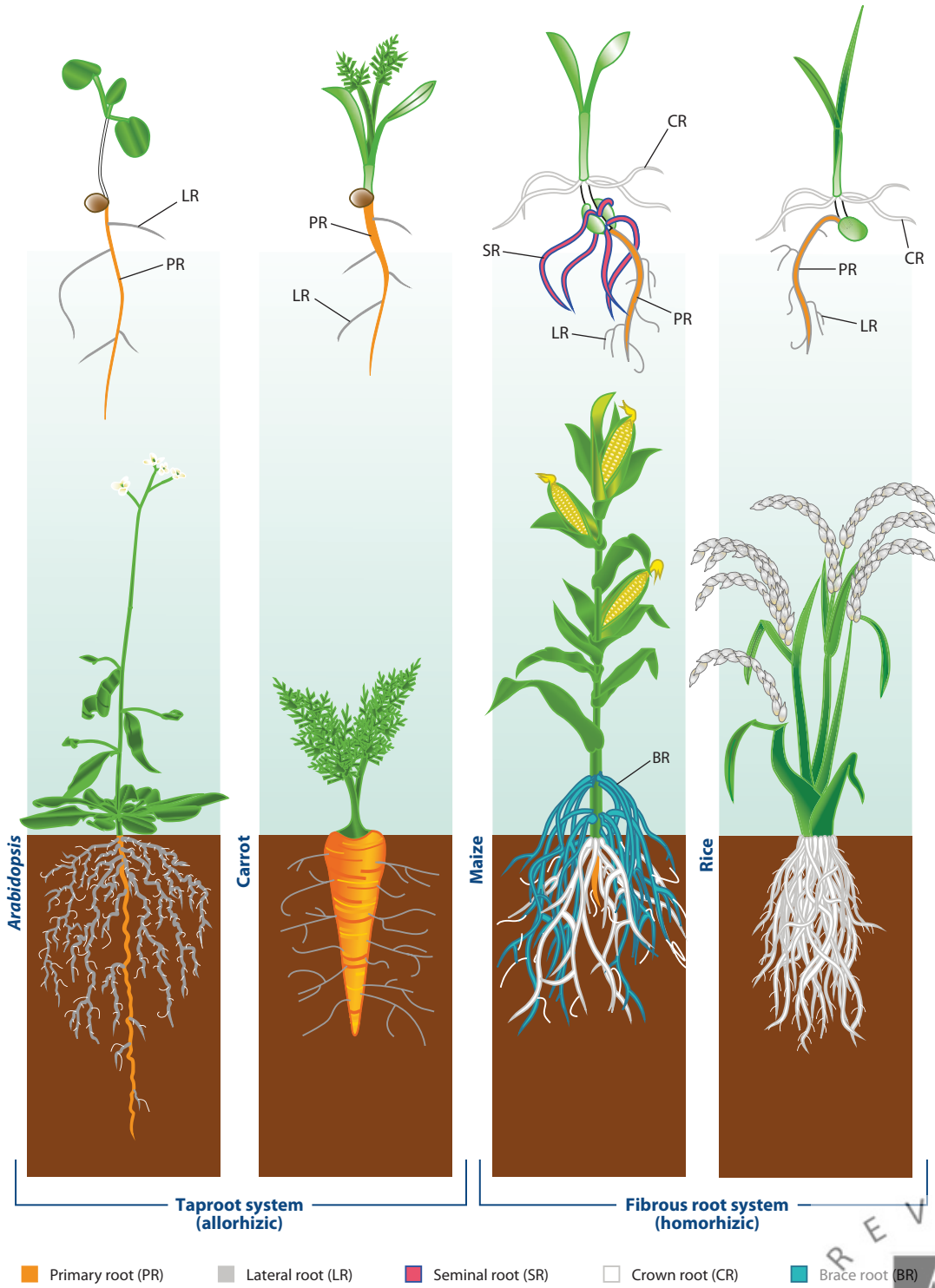In monocotyledons, the root system derived from the PR is small, short-lived, and important only in the early stages of seedling development. A new root system, called a fibrous root system or homorhizic system (**Figure 1**), develops from shoot-born roots, also called adventitious roots (ARs), which always develop postembryonically from shoots, stems, or leaves. In cereals such as maize (*Zea mays* L.) and rice (*Oryza sativa* L.), the postembryonic shoot-born roots are typically called crown roots (CRs) and brace roots (61) (**Figure 1**). The shoot-born roots of homorhizic systems can also branch by developing LRs. In monocotyledonous bulbous plants, such as onion (*Allium cepa*), garlic (*Allium sativum*), and tulip (*Tulipa* spp.), bulbs are used as the unit for vegetative propagation. Bulbs are composed of layers of modified leaves on a flattened stem that develops an adventitious fibrous root system for anchorage and uptake of water and nutrients (**Figure 2**). ARs also naturally develop in many dicotyledonous species, such as strawberries (*Fragaria* spp.) (**Figure 2a**), hops (*Humulus lupulus*), African violets (*Saintpaulia* spp.), and blackberries (*Rubus* spp.), which propagate vegetatively from stolons, rhizomes, leaves, and stems, respectively.

In both monocotyledons and dicotyledons, ARs can be induced either naturally [as an adaptive phenomenon to environmental changes such as flooding (90, 181) and dark–light transitions (54, 159) (**Figure 2b**)] or artificially [by wounding (cutting) (**Figure 2c**) and/or hormone application (1, 169)]. This ability of explants to form ARs is thus exploited in horticulture and forestry for mass production of cloned plants.

The Origins of Adventitious and Lateral Roots

Both ARs and LRs develop postembryonically. Nevertheless, although the origin of LRs is now well established and described in many species, the origin of ARs is much more variable and still largely undetermined, depending on the species and the organ or tissue they develop from.

LRs originate from pericycle cells of existing roots like the PR, earlier LRs, or ARs. Depending on the species, they may derive from pericycle cells adjacent to xylem pole cells (e.g., as in *Arabidopsis*, *Raphanus sativus*, and *Heliantus annuus*) or to phloem pole cells (e.g., as in maize and carrot) (15, 31). In cereals such as maize and rice, the endodermal cells also contribute to LR development and produce the epidermis and the root cap, whereas the pericycle cells are the source of all remaining tissues (39, 62). The different stages of LR initiation and development have been well characterized in the herbaceous model plant *Arabidopsis*. Starting from the first cell division in the pericycle cell up to the emerging LR primordium, seven stages have been identified that correspond to different steps in the acquisition of cell identity and tissue organization (93).

In contrast to LRs, ARs develop from different tissues and consequently from different cell types. A conserved feature is that ARs always develop from cells neighboring vascular tissues, whether they are part of the plant's development program (as in monocotyledons and naturally vegetatively propagated dicotyledons) or are artificially induced by wounding or hormone applications. Although histological studies have shown that specific cells become enlarged and subsequently undergo mitosis, the lack of early molecular markers makes identification of the original cell(s) much more difficult in ARs than in LRs. Observations have often been made of serial sections of shoot-derived organs from which ARs emerge, and the earliest stages that could be observed have so far not allowed investigators to precisely pinpoint whether one or more cells are the source of ARs; often, cell division had already started and/or small AR primordia were already formed.

ARs can initiate from hypocotyl pericycle cells, phloem or xylem parenchyma cells, young secondary phloem cells, or interfascicular cambium cells close to the phloem cells. In both maize and rice, cross sections in the coleoptile nodes indicate that CR primordia develop from cells
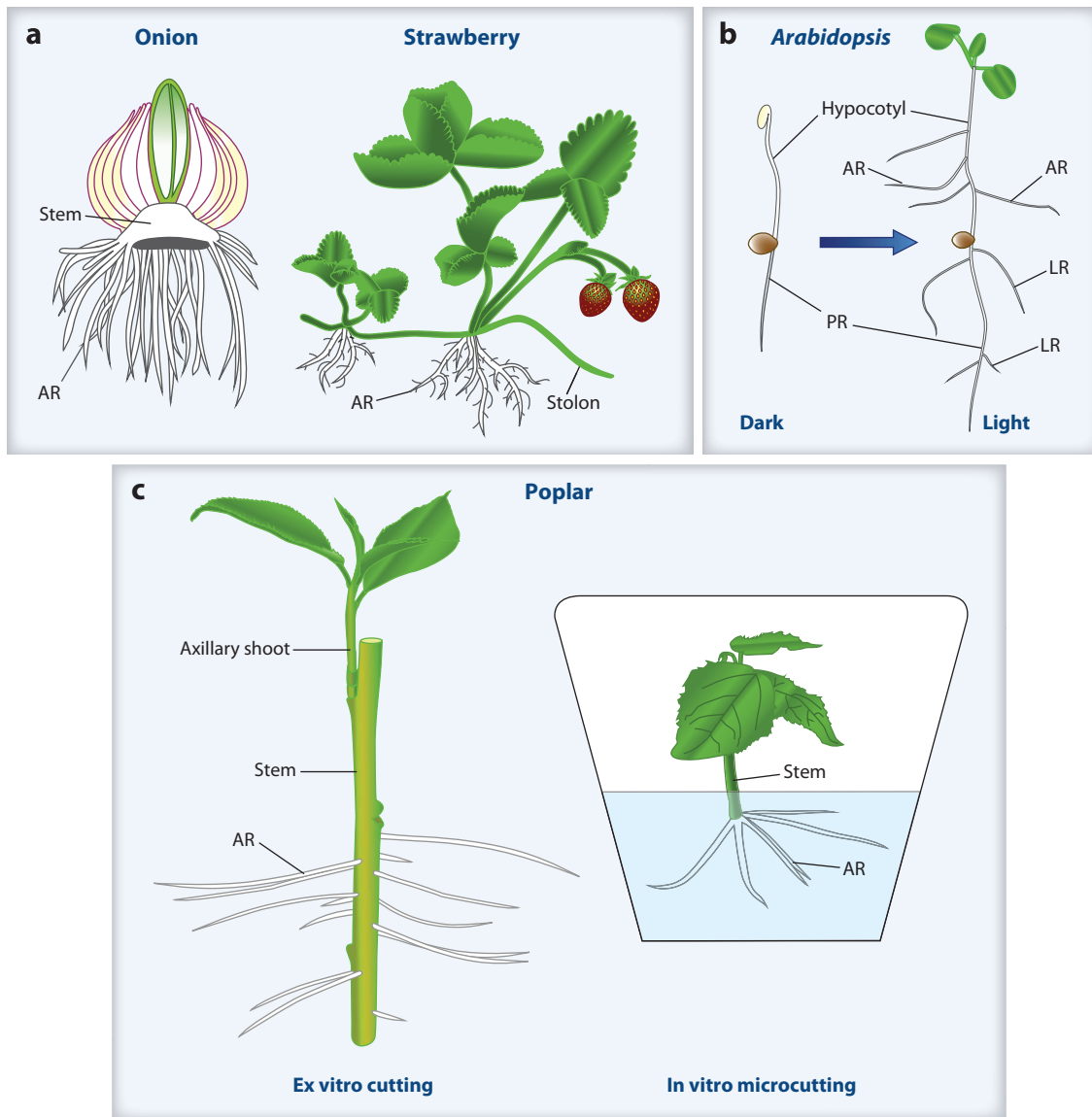
Figure 2

Schematic representation of adventitious root (AR) development. (*a*) Natural vegetative propagation by bulb (onion) or stolon (strawberry). (*b*) ARs induced by dark–light transition in *Arabidopsis*. (*c*) ARs induced by wounding in poplar. Additional abbreviations: LR, lateral root; PR, primary root.

close or adjacent to the vascular cylinder of the stem (60, 69). In *Arabidopsis*, ARs initiate from hypocotyl pericycle cells adjacent to the xylem pole, similarly to how LRs initiate (11, 169); from the vascular tissues (cambium and surrounding tissues) in derooted hypocotyls of older seedlings in which secondary growth has initiated; or from the vascular tissues of stem cuttings (25, 178). In woody perennials, ARs also emerge from cells close to the vascular system of the stem. In poplar stem cuttings, the AR primordia seem to emerge from the cells located at the

phloem/cambium junction (147), whereas in apple tree (*Malus domestica*) cuttings, ARs are initiated from interfascicular cambium cells adjacent to phloem cells (72, 110). ARs also originate from ray cells beside vascular bundles and leaf traces, as in red raspberry (*Rubus strigosus*) tip cuttings or in white pine (*Pinus strobus*) (58).

The development stages of ARs in vegetatively propagated dicotyledons (either annuals or perennials) are not as well described as those of LRs. Nevertheless, AR development has been divided into three successive but interdependent physiological phases: the induction phase, which precedes any histological event; the initiation phase, during which cell divisions lead to the formation of internal root meristems; and the expression phase, which corresponds to the internal growth of the AR primordia and emergence of the ARs (29). In most vegetatively propagated species, there are no cells specified to form ARs in stem cuttings before induction. In that case, an additional phase exists, which consists of the dedifferentiation of cells before their induction to become an AR. However, preformed AR initials (albeit dormant) already exist in the stems of some woody perennials, such as willow (*Salix* spp.) and poplar (58).

Clonal reproduction (creating progeny that are genetically identical to the original plant material) via rooted shoot-derived explants allows the production of elite clones, pest- or disease-resistant plants, or genetically improved trees for planting and breeding programs (58). Nevertheless, many economically and ecologically important tree species have a low capacity for AR formation and are categorized as difficult-to-root species. This feature makes them unsuitable for efficient large-scale commercial propagation through stem cuttings. Why such a difference between species exists is not understood. In the past few decades, significant progress has been made in understanding the physiology and molecular control of PR and LR development, mainly through studies of *Arabidopsis* (124, 132, 177). AR formation, in contrast, has proved difficult to study, and although impressive progress has been made in studying CR development in rice and maize (23, 63, 64), knowledge about the mechanisms controlling AR initiation and development from cuttings in dicotyledonous species is not as advanced.

The development of new technologies for genetic and molecular biological analysis of different species has opened new possibilities for investigation and consequently led to significant recent progress in understanding the environmental and endogenous control of AR formation. However, the data are still scattered, and there is a long way to go before the pieces of the puzzle come together. In this review, which does not aim to be exhaustive, we discuss in parallel what is now known about environmental or endogenous factors and related mechanisms controlling ARs and/or LRs, in order to highlight the differences and similarities as well as potential future directions in each area that could improve our knowledge of AR and LR development.

GENETIC ASPECTS OF ADVENTITIOUS AND LATERAL ROOT DEVELOPMENT

AR and LR development processes are complex heritable traits that are controlled by many endogenous regulatory factors and highly influenced by the environment. This underlies the genetic complexity of these traits. On the one hand, they are controlled by an endogenous genetic program that determines cell fate acquisition; cell division; and initiation of root primordia, emergence, and elongation. On the other hand, other sets of genes are important for sensing and responding to environmental cues such as gravity, light, drought, and biotic and abiotic stresses, and these explain the high phenotypic plasticity of the different root systems. In plants that are vegetatively propagated through cuttings, the response to the environment is important because it strongly conditions the physiological and biochemical quality of mother plants (125) and consequently influences the rooting capacity of the cuttings (48).

The characterization of *Arabidopsis* mutants altered in PR and LR development has been instrumental for dissecting the genetic and molecular networks controlling root development. This progress has been extensively reviewed (83, 129, 132), and genes involved in LR development are listed in **Supplemental Table 1** (follow the **Supplemental Material link** from the Annual Reviews home page at **http://www.annualreviews.org**). To a lesser extent, similar work has been performed in rice and maize, species where genes involved in either AR (CR) or LR initiation and development have been identified as well (**Supplemental Table 1**). Certain similarities in LR development, including conserved molecular regulatory elements, exist among these two species and *Arabidopsis* (reviewed in 123). Likewise, overlaps and/or similarities exist in the control of ARs and LRs (123) (**Supplemental Table 1**). Nevertheless, the fact that the *Arabidopsis* mutant *monopteros*, which totally lacks an embryonic PR, is able to develop normal ARs (134) and the existence of rice and maize mutants altered in the development of CRs but not PRs and LRs (and vice versa—mutants altered in the development of LRs but not CRs) (23, 64) suggest that specific regulatory mechanisms controlling AR initiation may exist. Indeed, research on LR development has outpaced that on AR development owing to the importance of LRs, and although information on LR development can inform understanding of AR development, the overlap between the two processes has only begun to emerge. Recent important advances in understanding genetic and molecular mechanisms related to AR formation have been made through studies of *Arabidopsis* mutants that allowed investigators to advance an initial model of the regulation of AR formation in *Arabidopsis* hypocotyls (54, 55, 159). However, whether it will be possible to translate what is known about AR development in herbaceous species to practical use in woody species—for which AR is a limiting step for vegetative propagation—is still an open question.

Because vegetative propagation capacity is important to many woody-species breeding programs, the potential offered by genetic variation in AR formation has been explored much earlier than that in LR formation. Comparison of genotypes with differing abilities to root from stem cuttings led to the identification of quantitative trait loci (QTLs) associated with the number of roots per rooted cutting in cottonwood (*Populus deltoides*) as early as 1968 (185). Since then, QTLs related to AR development have been reported for loblolly pine (*Pinus taeda* L.) (52), eucalyptus (*Eucalyptus* spp.) (51, 97), pedunculate oak (*Quercus robur*) (155), and poplar (194). Genetic variation for AR development has been also reported in herbaceous species such as *Arabidopsis*, in which different accessions responded differently to exogenous auxin (75); rapeseed (*Brassica napus*) (121); tomato (2); maize (95); and rice (68, 175, 198). LR development also shows high phenotypic plasticity in response to both biotic and abiotic environmental changes (92, 98) and at the intraspecific level, as illustrated by the variable root system architectures of diverse *Arabidopsis* accessions grown in the same conditions (103). The fully sequenced genome of *Arabidopsis* and the development of high-throughput mapping technologies made QTL analysis highly feasible in this model plant species and allowed the recent exploitation of natural variation and the identification of QTLs that influence root system architecture (44, 103, 156). Similarly, the recent release of genome sequences for *Eucalyptus grandis*, Norway spruce (*Picea abies* L.), and black cottonwood (*Populus trichocarpa*) (108, 118, 176) as well as the improvement of high-throughput genome-wide association studies and mapping will make cloning of QTLs in woody species accessible.

THE INFLUENCE OF ENVIRONMENTAL FACTORS ON ADVENTITIOUS AND LATERAL ROOT DEVELOPMENT

Roots are belowground organs that develop in the rhizosphere, which is a complex, heterogeneous environment where roots must interact with microorganisms (which are part of the biotic environment) and adapt to fluctuating abiotic modifications such as water availability and micro- and

macronutrient availability, concentration, and localization. The phenotypic plasticity of the root system reflects the fact that plants with identical genotypes adapt and modify their root system architectures based on the biotic and abiotic environment. The adaptation of plant root development in response to environmental changes has consequences for the physiological status of the aerial part that donates the organs for vegetative propagation. Therefore, the way roots adapt to their environment influences the capacity of shoot explants to develop ARs. The effects that environmental changes have on LR development were extensively reviewed recently (73, 124); therefore, we give only a brief overview and then compare these effects with the direct or indirect effects that environmental changes can have on AR development.

JA: jasmonate

IAA: indole-3-acetic acid

The Influence of Biotic Factors on Adventitious and Lateral Root Development

Most plants interact with beneficial symbiotic microorganisms, mainly mycorrhizal fungi and rhizobial bacteria; these interactions promote plant uptake of nutrients [e.g., nitrogen (N) and phosphorus (P)] and water and provide the microorganisms with relatively constant and direct access to carbohydrates. Importantly, interactions with microorganisms can induce major changes in the root system architecture by affecting general root growth, PR and LR length, LR number, and LR positioning and by stimulating AR development in hypocotyl or stem cuttings (18, 56, 88, 96, 115, 120, 122). Plants and microorganisms communicate through the secretion of signaling molecules (e.g., proteins, metabolites, or volatile organic compounds), which include plant hormones such as strigolactones, ethylene, jasmonate (JA), and auxin (14, 49, 161, 170, 190).

Interestingly, the root system architecture changes in response to presymbiotic signaling. For example, Olah et al. (120) showed that germinating spores of arbuscular mycorrhizal fungi stimulate LR development in *Medicago truncatula*, although they were separated from the roots, suggesting that the presence of molecules secreted by the spores could induce root initiation–related genes and set up a root development program. Maillet et al. (91) recently showed that the arbuscular mycorrhizal fungus *Glomus intraradices* secretes a mixture of lipochitooligosaccharides that stimulates root growth and branching in *M. truncatula*. Similarly, ectomycorrhizal fungi such as *Laccaria bicolor* and *Tuber melanosporum* can trigger LR formation prior to colonization in poplar (*Populus tremula* × *Populus alba*) and *Cistus incanus*, respectively, as well as in *Arabidopsis* (41, 162). This is likely due to fungal secretion of auxin, ethylene, and/or additional signaling molecules that modify the plant endogenous hormone homeostasis (41, 162).

Many compounds produced by fungi and plants have been identified (hormones, alkaloids, flavonols, and polyamines) and shown to play a role in symbiotic interactions either synergistically or antagonistically, but their impact on root development is not fully understood. Nevertheless, because most economically important trees form symbiotic relationships mostly with ectomycorrhizal fungi, these fungi have been tested as rooting agents both in vitro and ex vitro to stimulate adventitious rooting in the hypocotyl or stem cuttings of several difficult-to-root species. In most of these studies, the positive effect of AR formation was attributed to the plant hormone indole-3-acetic acid (IAA) produced by the fungi (reviewed in 116), which is often used exogenously to stimulate AR formation from cuttings. However, the amount of IAA produced by various fungi did not correlate with the rooting frequency or the number of ARs formed on cuttings during the interaction (114). This suggested that specific fungi produce additional compounds that act synergistically with or antagonistically to auxin in order to stimulate or inhibit AR formation. Indeed, filtrates from *Paxillus involutus* culture that contained low IAA concentrations promoted rooting of Scots pine (*Pinus sylvestris* L.) hypocotyls better than filtrates of *Pisolithus tinctorius* that contained more IAA (116). In addition to auxin, these fungi were shown to also produce polyamines: Both produced spermidine, and high concentrations of putrescine were found in

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P. involutus filtrates. Tang & Newton (171) later showed that spermidine significantly promotes the rooting frequency of Virginia pine (*Pinus virginiana* P. Mill.) cuttings. Likewise, spermidine and putrescine stimulated AR formation on micropropagated shoots of apple rootstock MM106 when added to the culture medium without auxin during the first day of the rooting process, but had no effect when added together with auxin (109). This is explained by the fact that the spermidine and putrescine modified the endogenous auxin metabolism of the shoot cutting (109).

Endophytic microorganisms are part of the biotic environment of plants. They reside within healthy plants without causing any damage and often even prove to be growth promoters (4) by providing beneficial compounds to host plants (87). Paz et al. (128) recently evaluated the rooting index, or efficiency, of *Eucalyptus urophylla* × *Eucalyptus grandis* hybrid stem cuttings after inoculation with several bacterial isolates from an *E. urophylla* × *E. grandis* hybrid. The results showed that the effect varied depending on the bacterium genotype, but several of the bacteria had a significant promoting effect on rooting. The mechanisms involved are still unknown, but they could be due either to the auxin produced by the microorganism or to the increased N fixation or P solubilization (128).

We are still far from fully understanding which molecular pathways are triggered during plant root development in response to microorganisms. However, recent studies have shed light on new factors interfering with the rooting process, and further research on the contribution of mycorrhizal fungi to AR initiation in forest tree cuttings is likely to identify new and specific regulatory molecular pathways. Likewise, more studies are required to better understand the benefit of endophytic microorganisms, because they might lead to the discovery of molecular pathways controlling AR development from stem cuttings.

Mineral Nutrition Is an Important Parameter for Adventitious and Lateral Root Development

The root system architecture is also dependent on the availability of macronutrients (N, P, potassium, calcium, magnesium, and sulfur) and micronutrients (boron, copper, iron, chloride, manganese, molybdenum, and zinc), the latter of which are essential for plant growth but required at a much lower concentration. All these nutrients are important for the plant, and the root architecture adapts to any change in concentration to optimize uptake. However, the two most limiting nutrients that have been shown to impact root development are N and P; therefore, in this section we focus on recent studies that have begun to elucidate the molecular mechanisms involved in the uptake, perception, and signaling pathways of N and P and the consequences for AR and/or LR development.

Adventitious and lateral root development in response to nitrogen supply. High-N conditions strongly inhibit PR and LR elongation, whereas low-N conditions enhance LR elongation. Nevertheless, N distribution in soil is not homogeneous, and in a globally low-N environment, a local high N concentration stimulates rather than inhibits LR growth. In *Arabidopsis*, the root response to exogenous N involves the (respectively) low- and high-affinity nitrate transporters *AtNRT1.1* and *-2.1* (*NITRATE TRANSPORTER 1.1* and *2.1*) and the nitrate-inducible MADS-box transcription factor *ANR1* (*ARABIDOPSIS NITRATE REGULATED 1*) (94, 195, 196). *AtNRT1.1* is induced by both auxin and nitrate and is important for nitrate uptake under high-N conditions (105). It was shown to be an auxin influx facilitator, and its activity as such depends on the nitrate concentration (78). In low-nitrate conditions, it promotes auxin transport out of the LR primordium and consequently represses LR development (78).

AtNRT1.1 was also suggested to be involved in the ANR1-mediated localized N response, which regulates the increased number of LRs in N-rich patches (142). AtNRT2.1 has been implicated in the control of LR initiation when the environmental carbon/nitrogen (C/N) ratio is high (94, 142). A high C/N ratio inhibits LR initiation in wild-type *Arabidopsis* plants, whereas the *lin1* (*lateral root initiation 1*) mutant, which is altered in *NRT2.1* expression, still produces LRs in the same conditions (94). In maize, a high nitrate supply inhibits root growth by modulating endogenous auxin content (174), and this inhibition is likely due to a reduction in nitric oxide content in the maize apical cells (197).

The direct impact of N nutrition on AR initiation still needs to be investigated. So far, the influence of the C/N ratio on the nutritional status of mother plants and the consequent effect on AR formation have been studied. Indeed, carbon assimilation, allocation, and partitioning within the plants are strongly influenced by any modification in N supply. Druege et al. (37) showed that AR formation in pelargonium (*Pelargonium* spp.) cuttings is significantly affected by the initial C/N ratio. A high N supply to a mother plant grown under high-light conditions results in increased endogenous N content, which has a positive effect on rooting of cuttings of pelargonium and poinsettia (*Euphorbia pulcherrima* Willd.) after storage under low light. Nevertheless, this effect is conditioned by carbohydrate availability, because in cases of low initial endogenous sugar content, high N either has no effect or inhibits AR formation (37, 193).

Nitric oxide is another signaling molecule that derives from N metabolism and has been implicated in various plant physiological and developmental processes, including PR, AR, and LR development. Nitric oxide has been reported to be involved in the regulation of PR elongation and LR initiation in tomato plants (20, 21). Correa-Aragunde et al. (20) showed that it controls cell division during the early stages of LR primordial formation by mediating the induction of the *CYCD3;1* (*CYCLIN D3;1*) gene and the repression of the CDK inhibitor gene *KRP2* (*KIP-RELATED PROTEIN 2*). Pagnussat et al. (126, 127) showed that nitric oxide is also involved in auxin-induced AR root development in cucumber (*Cucumis sativus*) and that cGMP-dependent and cGMP-independent signaling pathways regulate the formation of a new AR system. The cGMP-independent pathway involves a mitogen-activated protein kinase signaling cascade that regulates cell division in a calcium-dependent way (81).

Phosphorus deficiency promotes adventitious and lateral root initiation and elongation.

P is present in the soil in the form of inorganic phosphate (P_i), and because it forms insoluble complexes with cations, particularly aluminum and iron under acidic conditions and calcium under alkaline conditions, its availability can be very low. Therefore, P rapidly becomes a limiting nutrient, and P starvation triggers a set of plant adaptive responses aimed at optimizing P_i usage (149). Upon P_i starvation, the root system is greatly modified, and most plants tend to develop a shallower root system with a shorter PR and an increased density of longer LRs. These adaptive modifications are developed by the plants to explore upper soil layers (topsoil foraging), where P_i tends to accumulate.

The formation of arbuscular mycorrhiza or ectomycorrhiza with symbiotic fungi is an efficient and widespread response that favors P_i uptake (130); likewise, endophytes can participate in P_i solubilization that facilitates assimilation (87). Alternatively, plants from some families develop so-called cluster roots (highly branched clusters of LRs just below the soil surface) and secrete phosphatases and organic acid to solubilize P_i for better uptake (153). In most plants, low P_i inhibits PR elongation and concomitantly stimulates LR density and elongation. However, this is not a general response, and intra- and interspecies genetic variation occurs (9, 27, 65, 84, 99, 143, 199). In maize, the response to P_i starvation is genotype dependent, with some genotypes showing an increased number of longer LRs and others showing the opposite phenotype (9, 84).

In rice, P_i starvation slightly stimulates PR elongation, inhibits LR development, and enhances AR initiation rate and elongation (27, 65, 199). Similarly, AR development is controlled by P availability in intact common bean plants (*Phaseolus vulgaris* L.) in a genotype-dependent manner (99). ARs enhance P acquisition because they have a shallow growth angle that allows them to explore the topsoil layers more efficiently. Ochoa et al. (119) identified two major QTLs that account for up to 61% of the total phenotypic variation in adventitious rooting traits under low-P conditions.

The role of P nutrition of stock plants in vegetative propagation or during the rooting phase has not been investigated in depth. Modification of mineral nutrition during in vitro culture of *Eucalyptus globulus* microshoots highlighted phase-specific mineral nutrient compositions optimized for the cuttings themselves (154). P deficiency in the culture medium resulted in significant reductions of AR density and elongation (154). As mentioned above, Paz et al. (128) also showed that the rooting efficiency of *E. urophylla* × *E. grandis* hybrid stem cuttings improved after inoculation with several bacterial isolates from an *E. urophylla* × *E. grandis* hybrid. This promoting effect was likely partially explained by improved P_i nutrition due to better solubilization of P_i. Another recent study showed that increased P fertilization of olive tree (*Olea europea* L.) stock plants significantly increased the proportion of rooted cuttings but had no effect on cutting survival (26).

In the past 10 years, thanks mainly to the characterization of several *Arabidopsis* mutants affected in their response to exogenous P concentration, studies have shed light on the complex P_i sensing and signaling mechanisms. The corresponding results have been extensively reviewed (17, 117, 149); therefore, here we give only a brief overview of recent findings related to the role of P_i in AR and LR development.

Two signaling pathways exist: local signaling, which is dependent on the external concentration of P_i, and systemic or long-distance signaling, which is determined by the P_i status at the whole-plant level. Most changes observed in root system architectures seem to be driven by the local sensing route independently of the endogenous P_i content (172). *Arabidopsis* and rice genes identified so far as involved in the stimulation of LR and/or AR formation under low-P_i conditions are listed in **Supplemental Table 1**. In *Arabidopsis*, P_i-induced LR development seems to require the auxin signaling pathway, which involves the auxin receptor TIR1 (TRANSPORT INHIBITOR RESPONSE 1) and the transcription factors SLR (SOLITARY ROOT)/IAA14 and ARF7 and -19 (AUXIN RESPONSE FACTOR 7 and 19) acting downstream of TIR1 and which modulates the expression of genes regulating the pericycle cell division and LR development (111, 131).

Ethylene has also been implicated in the modification of the root system architecture under P_i starvation. Analyses of ethylene signaling mutants showed that during P_i starvation, ethylene was important for the promotion of LR elongation but was not required for LR initiation (89). Several transcription factors involved in the P_i signaling pathway have also been identified, including members of the basic helix-loop-helix, MYB, and WRKY families, several of which are involved in root development (27, 32, 33). P_i is part of the nutrient-complementing culture media used for rooting cuttings; therefore, in addition to the knowledge acquired about the influence of the P_i status of the mother plant, the endogenous P_i signaling pathways may help to optimize P_i concentration in culture in order to establish more favorable rooting conditions.

Light is an important environmental parameter that impacts both adventitious and lateral root development. Light is an important parameter that has long been considered in vegetative propagation practices when optimizing conditions for rooting cuttings. Since the early 1980s, considerable effort has also been devoted to studies related to the effects of light versus darkness, focusing mainly on the enhancing effect of darkness on root formation in woody-plant cuttings (36, 57, 76). Several studies have focused on the effects of light intensity and/or quality on rooting

of cuttings (7, 28, 43, 46, 71) and highlighted possible synergistic or antagonistic effects with plant growth regulators such as auxin and cytokinins (CKs) (7, 43, 71, 189), suggesting the involvement of photoreceptors in the regulation of AR and likely LR development.

Recent studies performed with *Arabidopsis sur2* (*superroot 2*) and *ago1* (*argonaute 1*) mutants, which are altered in their ability to form ARs, suggested how light and auxin could potentially interact in the regulation of adventitious rooting (159). *ago1* mutants are defective in light-regulated hypocotyl elongation and auxin-induced AR formation but not in LR formation. The defect in AR formation in *ago1* mutants correlated with an alteration of auxin homeostasis in the apical part of the seedling and a hypersensitivity to light. Hypersensitivity to light was partially restored in the *ago1 phyA* (*phytochrome A*) double mutant, suggesting that the PHYA signaling pathway was upregulated in the *ago1* mutant (159). Gutierrez et al. (54) showed that light positively regulates the expression of the transcription factor genes *ARF6* and *ARF8* and negatively regulates the expression of *ARF17*, which positively and negatively control AR initiation in *Arabidopsis* hypocotyls, respectively. However, further investigation is needed to identify which light signaling pathway regulates the expression of these *ARF* genes.

Other studies of *Arabidopsis* have demonstrated that roots have photoreceptors for blue, red, and far-red light (reviewed in 73). In *Arabidopsis* roots, the phototropin PHOT1 mediates the negative phototropic response to blue light (47), the root-expressed PHYA and PHYB mediate the positive phototropic response to red light, and PHYA promotes root elongation under far-red light (22). Both root growth responses to shoot light exposure and AR initiation in the aerial parts of plants might be related to modification of local endogenous auxin concentration. Indeed, auxin action depends on tightly regulated distribution across the plant. Auxin is transported from cell to cell in a polar manner through the concerted action of several carrier proteins. It was recently demonstrated that the expression and/or localization of the efflux carrier proteins PIN1, -2, and -3 (PIN-FORMED 1, 2, and 3) is regulated by light (35, 150). In addition, Sibout et al. (158) showed that the basic leucine zipper transcription factor HY5 (LONG HYPOCOTYL 5), which acts downstream of the light receptor network and whose activity is controlled by the RING E3 ubiquitine ligase COP1 (CONSTITUTIVE MORPHOGENIC 1), controls the genes related to auxin signaling. Thus, the increased AR and LR development observed in the *hy5* mutant is likely due to a modification of the auxin signaling pathways.

EFFECTS OF ENDOGENOUS FACTORS ON THE CONTROL OF ADVENTITIOUS AND LATERAL ROOT DEVELOPMENT

Aging Is a Limiting Factor for Adventitious Rooting

During development, most plants undergo phenotypic changes that are more or less dramatic in different species; these changes are part of an ontogenetic process known as phase change or maturation. This process can be divided into three phases: the juvenile vegetative phase, the mature vegetative phase, and the reproductive phase. Although transition to flowering is an indicator that the maturation stage has been achieved, other phenotypic changes—e.g., changes in leaf shape, shoot orientation, and stem pigmentation and a decrease in rooting competence—occur during the transition from the juvenile vegetative phase to the mature vegetative phase (133).

In forest, fruit, and ornamental trees, the loss of rooting competence is one of the most economically important factors that limit clonal propagation of genetically improved elite genotypes. A study comparing the rooting processes of chestnut (*Castanea sativa*) shoots from the same genotype but with either juvenile (easy-to-root) or mature (difficult-to-root) characteristics showed that there were no anatomical differences in the mature shoots and that the reactivation of cell

division in response to exogenous auxin took place in both juvenile and mature shoots (5). However, no meristem organization was observed in the mature cuttings. The endogenous auxin content was not the limiting factor, because both cuttings retained the same level of IAA. Vidal et al. (179) obtained similar results in a comparison of in vitro–derived oak (*Quercus* sp.) shoot cultures established from material simultaneously collected from crown and basal shoots of 100–300-year-old trees. In both cases, the endogenous level of auxin was unchanged and the cell division was triggered by exogenous auxin, indicating that tissues from mature cuttings retain the same capacity to undergo cell division, but no dedifferentiation followed by redifferentiation occurred. Interestingly, the maturation phase of the shoot or whole plant can be reversed to the juvenile phase through several reinvigoration techniques, including sequential grafting of adult scions onto juvenile rootstocks, which can reestablish the rooting potential of adult shoots (67).

What cellular and biochemical modifications occur during maturation and phase changes and how these events reconfigure molecular pathways that lead to the inhibition of AR initiation in mature tissues are still open questions. However, recent studies have uncovered several potential mechanisms. A prevalent theory explaining maturation-related changes is that they reflect changes in DNA methylation. A comparison of the DNA methylation in samples from juvenile and mature chestnut cuttings showed that aging was related to a progressive increase of methylated 5-deoxycytidines (59). An opposite trend was observed in microshoots of *Acacia mangium* and *Sequoiadendron giganteum*, in which DNA from juvenile shoots was more methylated than DNA from shoots with mature leaves (8, 100). Repeated grafting of adult shoot scions of coast redwood (*Sequoia sempervirens*) onto juvenile rootstock resulted in the progressive restoration of juvenile traits and rooting competence owing to progressive reduction in DNA methylation (66).

Studies of *Arabidopsis* might also open new directions for investigation. Using derooted hypocotyls of young (12-day-old) and adult (26-day-old) plants of the Landsberg *erecta* (L*er*) ecotype, Díaz-Sala et al. (34) showed that AR development was significantly reduced in adult derooted plants. Exogenously applied auxin did not stimulate rooting of derooted adult plants, and the endogenous auxin level was not the limiting factor. In contrast, decreases in AR development in derooted hypocotyls of *Arabidopsis* adult plants was dependent on certain peptides bearing the Arg-Gly-Asp signature, called RGD peptides: The rooting percentage of adult derooted plants increased upon application of RGD peptides, whereas there was no effect on juvenile plants.

The connection between phase changes and epigenetic gene regulation has been further confirmed by the fact that several *Arabidopsis* mutants affected in phase change were also altered in the genesis of small RNAs (19–24-nucleotide RNAs), including both microRNAs and short interfering RNAs (186). The transition from the juvenile vegetative phase to the mature vegetative phase was later shown to be regulated by miR156 (188), a microRNA that is conserved throughout the plant kingdom (3) and that controls the expression of SBP/SPL (SQUAMOSA PROMOTER BINDING PROTEIN-LIKE) transcription factors (188). miR156 is necessary and sufficient for the expression of the juvenile phase and regulates the timing of the juvenile-to-adult transition by coordinating the expression of several pathways that control different aspects of this process (187). Whether the loss of competence to develop ARs associated with the phase change is also under the control of miR156 is unknown but remains an obvious possibility for investigation.

The Role of Phytohormones

An increasing amount of evidence from genetic analysis indicates that the impact of biotic and abiotic changes on root system architecture, including PR, AR, and LR development, results from modulation of the endogenous factors' homeostasis and/or signaling (92, 124). Among the endogenous factors, the phytohormones are the most important modulators of root development.
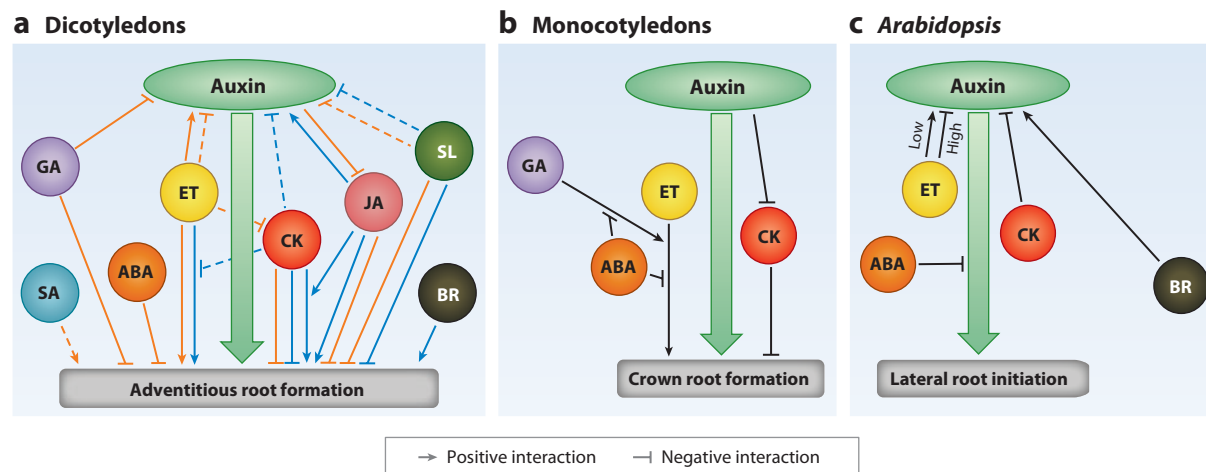
Figure 3

Hormonal cross-regulatory interactions in the regulation of adventitious root formation in various plant species compared with those of lateral root initiation (before primordium emergence) in *Arabidopsis thaliana*: (*a*) adventitious root formation in various dicotyledons, (*b*) crown root formation in various monocotyledons, and (*c*) lateral root initiation in *Arabidopsis*. Various phytohormones, including ethylene (ET), cytokinins (CKs), gibberellic acid (GA), abscisic acid (ABA), strigolactones (SLs), brassinosteroids (BRs), salicylic acid (SA), and jasmonate (JA), have been shown to influence root development directly, by interacting with each other, or by interacting with auxin. Dashed lines represent possible links that have not been fully demonstrated. In panel *a*, orange lines show hormonal interactions during adventitious root formation in intact plants, and blue lines show interactions in cuttings and alternative rooting systems.

It has now become obvious that they interact with one another (**Figure 3**) and with environmental cues in complex networks in which auxin plays a central role (83). **Figure 3** summarizes the roles of different hormones in the early stages of AR and LR formation.

The role of auxin in adventitious and lateral root development. Auxins are a group of plant growth regulators that include both naturally occurring and synthetic chemicals. The most studied natural auxins are IAA and indole-3-butyric acid (IBA). Auxin is involved in every aspect of root development in both monocotyledons and dicotyledons, from cell fate acquisition to meristem initiation, emergence, and elongation. Characterization of *Arabidopsis*, rice, and maize mutants altered in LR development has helped identify components of the polar auxin transport and auxin signaling pathway required at each step of LR and CR development (23, 83, 123, 132, 141, 182) (**Supplemental Table 1**). Endogenous polar auxin transport is also required for AR initiation in hypocotyl or stem cuttings of several species (24, 169), and the ABCB19 (ATP-binding cassette B19) auxin efflux transporter seems to play a significant role in *Arabidopsis* hypocotyls (169). Recent studies in *Arabidopsis* showed that IAA is likely to induce AR initiation through the activation of an auxin signaling network similar to that in LR or CR initiation (54, 55) (**Figure 4**).

Although IAA is the most abundant natural auxin and was the first used to stimulate AR development on stem cuttings (19), it is not routinely used in vegetative propagation programs, where IBA is preferred. When added exogenously, IBA is an efficient promoter of AR in many species, and it likely acts after its conversion to IAA, which has been shown to occur in many species (79, 151, 168). For a long time, IBA was thought to be a more efficient stimulator of AR initiation in stem cuttings because of its increased resistance to light-induced degradation compared with IAA. Nevertheless, recent studies suggest that IBA, which has long been known to move great distances in plants, might use transporters that are distinct from those used by IAA. AUX1 acts as

IBA: indole-3-butyric acid

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17.14
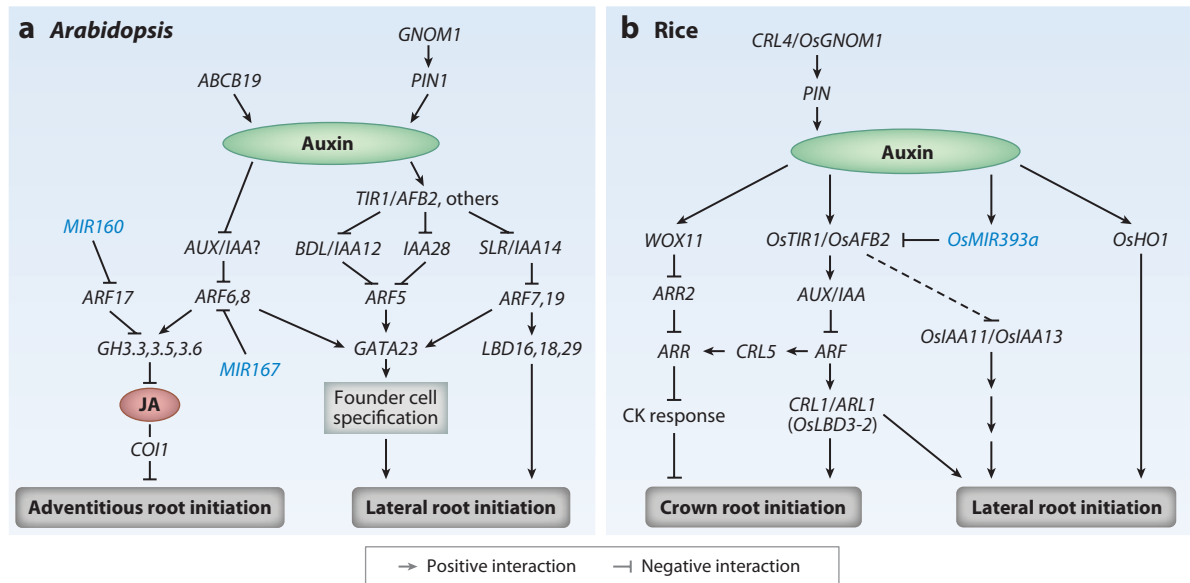
Figure 4

Genetic cross-regulatory networks controlling (*a*) adventitious and/or lateral root initiation in *Arabidopsis* and (*b*) crown and/or lateral root initiation in rice. Auxin plays a central role in both developmental processes in these species. The names of genes are in black text, the names of genes encoding microRNA names are in blue text, and hormones are inside colored ovals. Dashed lines represent possible links that have not been fully demonstrated. Gene abbreviations: *ABCB19, ATP-binding cassette transporter B19*; *AFB2, AUXIN SIGNALING F-BOX 2*; *ARF, AUXIN RESPONSE FACTOR*; *ARL1, ADVENTITIOUS ROOTLESS 1*; *ARR, type-A RESPONSE REGULATOR*; *AUX/IAA, auxin/indole-3-acetic acid*; *BDL, BODENLOS*; *COI1, CORONATINE INSENSITIVE 1*; *CRL, CROWN ROOTLESS*; *GATA23, GATA transcription factor 23*; *GH3, Gretchen Hagen 3* (encoding the GH3 auxin-inducible acyl-acid-amido synthetase); *GNOM1*, gene encoding a membrane-associated ARF-GEF (guanine nucleotide exchange factor of the ADP-ribosylation factor G protein); *HO1, HEME OXYGENASE 1*; *LBD, LATERAL ORGAN BOUNDARIES DOMAIN*; *PIN, PIN-FORMED* (encoding the PIN auxin efflux carrier protein); *SLR, SOLITARY ROOT*; *TIR1, TRANSPORT INHIBITOR 1*; *WOX11, WUSCHEL-Related Homeobox 11*. Other abbreviations: CK, cytokinin; JA, jasmonate; MIR, microRNA; *Os, Oryza sativa*.

an influx carrier for IAA but not for IBA. Similarly, PIN2, PIN7, ABCB1, and ABCB19 act as efflux carriers for IAA but not for IBA. In contrast, the PDR (PLEIOTROPIC DRUG RESISTANCE) family proteins ABCG36 and ABCG37 appear to efflux IBA but not IAA (167). In addition, IBA is not degraded or converted to IAA during its long-distance transport (168), suggesting that the independent transport systems may provide a mechanism to specifically move the inactive precursor to a specific site of action, avoiding auxin responses during transport. These interesting results point toward new possible routes of investigation to understand the higher efficiency of IBA in stimulating AR initiation in stem cuttings.

Cytokinins. CKs are a class of plant growth regulators known to promote cell division and shoot development. They are antagonistic to auxin and suppress rather than promote AR and LR formation in many species, including *Arabidopsis*, rice, alfalfa (*Medicago sativa*), and poplar (50, 82, 135, 136, 184) (**Figure 3**). Nevertheless, low CK concentrations are beneficial during the early stages of AR initiation in apple (*Malus pumila* Mill.) and Monterey pine (*Pinus radiata*) cuttings (144, 145) (**Figure 3***a*). In *Arabidopsis*, lines overexpressing CK oxidase/dehydrogenase–encoding genes have reduced endogenous CK levels and an increased frequency of ARs and LRs (184), and mutants altered in the expression of CK receptors have an increased frequency of LRs (146). CKs

modify the expression of auxin polar transport genes (*PIN* genes), preventing the formation of the required auxin gradient in the LR founder cells and thereby inhibiting the initiation of LR primordia (82) (**Figure 3c**). Another study showed that zeatin riboside, one species of cytokinin present in xylem sap, is the main suppressor of AR formation in *Arabidopsis* hypocotyls (80). The cytokinin receptors are required for the formation of auxin-transporting vascular tissues in hypocotyls, which is necessary for LR development but not for AR development (80). These results imply that different and specific mechanisms controlling vascular development in ARs and LRs exist. Comparative transcriptomics between ARs and LRs could be a way to identify specific regulators.

Ethylene. The role of ethylene in AR and LR formation is subtle and complex, as ethylene biosynthesis is controlled by auxin and vice versa. In addition, ethylene regulates auxin transport and signaling (166). Auxin and ethylene act either antagonistically or synergistically and have opposite effects on ARs and LRs (104, 166) (**Figure 3**). *Arabidopsis eto1* (*ethylene overproducer 1*), *Arabidopsis ctr1* (*constitutive triple response 1*), and tomato *epi* (*epinastic*) mutants develop fewer LR roots than wild-type plants, whereas *Arabidopsis ein2* (*ethylene insensitive 2*) and tomato *Nr* (*Never ripe*) mutants, which are completely insensitive to ethylene, develop more LRs than wild-type plants (112). In contrast, ethylene promotes AR formation in tomato hypocotyls. Both the negative effect on LRs and the positive effect on ARs are likely to occur through differential modulation of auxin transport (112).

Ethylene also positively regulates AR formation in flooded tomato plants (180), and a promoting role of ethylene in AR development has been reported in species such as sunflower (*Helianthus annuus*), apple, mung bean (*Vigna radiata*), and petunia (*Petunia* sp.) (reviewed in 48, 79), potentially as a result of auxin–ethylene crosstalk. Ethylene also interacts with other hormones, as shown by the complex interaction between ethylene, gibberellic acid (GA), and abscisic acid (ABA) in the control of AR formation in deepwater rice. GA was ineffective on its own but had a synergistic effect with ethylene to promote ARs, and ABA acted as a competitive inhibitor of GA activity (164).

Abscisic acid. ABA has been described as a negative regulator of ARs, CRs, and LRs (**Figure 3**), although few studies have reported a positive effect, suggesting that subtle interactions might occur, possibly depending on the development phase. ABA is a negative regulator of AR development in both tomato and rice (**Figure 3a,b**). The ABA-deficient tomato mutants *flacca* and *notabilis* produce an excess of ARs on the stems. The AR phenotype of the *notabilis* mutant could be restored to wild-type phenotype by expressing an *SpNCED1* gene involved in ABA biosynthesis (173). In flooded rice plants, the balance between ethylene, GA, and ABA is altered upon submergence, and ABA was identified as a hormone that negatively controls AR emergence, which was reduced to approximately 50% upon ABA treatment (164). In *Arabidopsis*, exogenously applied ABA significantly inhibits LR development immediately after the emergence of the LR primordia, and this inhibition was suggested to be auxin independent (30). In contrast, the *Arabidopsis abi3* (*abscisic acid insensitive 3*) mutant is resistant to auxin-induced root initiation and to auxin transport inhibitors, suggesting crosstalk between auxin and ABA for the regulation of LRs (12). Similarly, ABA induces LR initiation in rice (16). However, the *ABI4* gene, which encodes an ABA-regulated AP2 (APETALA 2) domain transcription factor, mediates ABA and CK inhibition of LR development in *Arabidopsis* by controlling polar auxin transport (157).

Gibberellins. Although no major role of GA in the control of LR development has been reported, GA biosynthesis has been detected in the root tips of different plants, and GA signaling is required

for PR growth of *Arabidopsis* and rice (45, 74). In contrast, GAs have a negative effect on AR formation. Exogenously applied GA inhibits AR formation in rice plants, whereas rice mutants deficient in GA biosynthesis develop more ARs (85). Similar results were observed in poplar (13). Likewise, the tomato *pro* (*procera*) mutant, in which GA signaling is constitutively active, has a very poor regeneration capacity in a root-inducing medium (86). In one case, GAs acted synergistically with ethylene to promote initiation and growth of ARs in deepwater rice plants (164). Whether this interaction is specific to flooded plants is not known.

Jasmonate. JA is a stress-related hormone whose role in plant development emerged recently. JA interacts with auxin at different levels by modulating its biosynthesis or transport (reviewed in 183), and as with auxin signaling, the AXR1 (AUXIN RESISTANT 1)–dependent modification of the CULLIN 1 subunit of the SCF^{COI1} complex is required for JA/JA-isoleucine signaling (191). JA has an inhibitory effect on PR development, likely by interacting with auxin (reviewed in 183). Likewise, although auxin stimulates LR initiation, the tryptophan-conjugated forms of JA and IAA inhibit LR formation, indicating a potential biological activity for hormone conjugates (163). In addition, the *Arabidopsis* JA-insensitive mutant *coi1-16* (*coronatine insensitive 1-16*), which is altered in expression of the JA receptor, produces fewer LRs and shows increased expression of JA biosynthetic genes in emerging LRs, strongly supporting the role of JA in LR formation (165). Similarly, JA inhibits AR initiation in *Arabidopsis* hypocotyls through the COI1 signaling pathway (55) (**Figure 4**). In contrast, under in vitro conditions in the presence of exogenous auxin, JA had a synergistic promoting effect on AR formation in potato (*Solanum tuberosum*) stem cuttings (140) and tobacco (*Nicotiana tabacum*) thin cell layers (40). These apparent contradictions suggest that the balance between auxin and JA, as for other hormones, is a crucial factor to be considered in addition to the development phase. In conclusion, there is now substantial evidence supporting the role of JA in LR and AR formation, but further investigation is required to determine whether it acts through the same or a similar regulatory pathway in both root systems.

Brassinosteroids. Most brassinosteroid biosynthesis and signaling mutants have a pleiotropic dwarf phenotype, and it is therefore difficult to estimate whether an associated root phenotype is due to a primary effect. Many auxin signaling genes involved in root growth and development are induced by both auxin and brassinosteroids. Like auxin, brassinosteroids promote PR growth at low concentrations but inhibit it at higher concentrations (107). They also control LR development through a complex interplay with auxin (6, 103, 113). Similar to *Arabidopsis* brassinosteroid-deficient mutants, rice mutants affected in brassinosteroid biosynthesis, such as *brd1* (*brassinosteroid-dependent 1*), show a significant reduction in brassinosteroids and abnormal root morphology phenotypes, which were restored by exogenously applied brassinosteroids (102). Thus, although the precise mechanism of their activity is unclear, brassinosteroids appear to promote LR development through interactions with endogenous auxins. Whether they also interact with auxin in the process of AR formation is not clear, although an early study showed a significant improvement in the rooting capacity of Norway spruce cuttings (148).

Strigolactones. Strigolactones are a recently recognized class of plant hormones that inhibit bud outgrowth; they have recently been described as negative regulators of AR and LR development in different species, including *Arabidopsis*, tomato, pea, and maize (53, 77, 137–139). They likely act in interaction with ethylene, CKs, and auxin. Recent studies in *Arabidopsis* and pea indicate that basipetal auxin transport and auxin accumulation in the rooting zone may be negatively regulated by strigolactones (139). The role of strigolactones in root development is a new area of

investigation and will likely provide additional insights about hormone crosstalk in the regulation of root growth.

Peptide hormones. Multicellular organisms regulate cell–cell interactions through the use of peptide hormones, which are small peptides that act as signaling molecules. These hormones regulate and coordinate cell functions and have large implications for plant development. Produced in one cell and perceived in the neighboring cell, they function on a small cell-to-cell scale (192). The role of hormone peptides in the shoot apical meristem has been well characterized and documented (reviewed in 106), but their role in root development has only begun to emerge (192). Among the GLV (GOLVEN)/RGF (ROOT GROWTH FACTOR)/CLE (CLAVATA 3/EMBRYO SURROUNDING REGION) signaling peptides, some control the maintenance of the root meristem, gravitropic response, and local auxin redistribution (192). Several *GLV* genes are expressed at early stages during LR development. When overexpressed in transgenic plants, they strongly inhibit LR development (42). Thus, hormone peptides are likely to be important players in controlling cell–cell interactions during PR and LR development. Which signaling pathways, receptors, and downstream targets are involved are still open questions. Because of their mode of action, peptide hormones likely also play a role in AR development, but this still needs to be investigated.

MOLECULAR ASPECTS OF ADVENTITIOUS AND LATERAL ROOT FORMATION

The above description of factors influencing AR and LR development shows the complexity of the interactions and underlines the fact that root development and its response to environmental changes are controlled by complex gene regulatory networks. In parallel to the physiological and genetic characterization of mutants and/or transgenic plants in different species (but mainly in *Arabidopsis*), genome-wide analysis describing the *Arabidopsis* transcriptome, proteome, and metabolome allowed the identification of gene regulatory networks (reviewed in 101). Expression maps providing a three-dimensional representation of genes, metabolites, or proteins in roots have also been useful for studying expression patterns in a particular cell type or organ in response to the environment (152). *Arabidopsis* transcriptional expression maps have also been used to reconstruct gene regulatory networks that led to predictive transcriptional modules, some of which have been demonstrated experimentally (160).

A combination of all these approaches led to the functional characterization of the multiple auxin signaling modules that regulate LR development, from cell specification to LR primordium emergence, in *Arabidopsis* (reviewed in 83, 129). The availability of whole-genome and transcriptome sequences as well as proteomic analysis in crop and tree species will allow comparative analysis and certainly help identify genes and networks in other species as well (70). Characterization of rice and maize mutants altered in AR and LR development showed that the transcriptional regulatory pathway involving TIR1/AFB2 (AUXIN SIGNALING F-BOX 2) auxin receptors and the AUX/IAA, ARF, and LBD (LATERAL ORGAN BOUNDARIES DOMAIN) transcription factor proteins are conserved in cereals and *Arabidopsis* (reviewed in 123) (**Figure 4**). Interestingly, this rice pathway controls initiation of ARs and CRs but not LRs. Whether a similar pathway exists in rice for LRs remains to be demonstrated.

These results show that similar mechanisms are likely regulating AR and LR development, although they originate from different organs. This was confirmed by recent results showing that in *Arabidopsis* hypotocyls, AR initiation is regulated by a similar transcriptional module that involves three ARF proteins (54, 55), two of which are also involved in LR initiation (**Figure 4**).

These results bring hope to researchers working to better understand the molecular mechanisms that control AR initiation. Whether the data obtained on herbaceous plants will be transposable to woody species is an open question and needs further investigation.

CONCLUSIONS

Although our understanding of the development, regulation, and environmental adaptation of ARs has greatly improved in the past few years, it is still not as comprehensive as our understanding of PR and LR development. The information is still scattered and difficult to process. As with studies of PR and LR development, *Arabidopsis* has already proven useful as a model system to dissect the molecular mechanisms controlling ARs, and further research in this direction will certainly lead to the identification of additional pieces of the puzzle. However, there are fundamental and practical specificities that are inherent to particular species—in particular, in the case of trees, both angiosperms and gymnosperms. Rooting cuttings for vegetative propagation requires considering several parameters, including the ages of the plants, their nutritional status, and their growth conditions. All of the parameters reviewed above have an impact on rooting competence. Global approaches similar to those developed for *Arabidopsis* might therefore be useful to improve our knowledge and find a way to optimize conditions for better rooting of recalcitrant species. The development of the new -omics technologies and the availability of transcriptomes, proteomes, and metabolomes will make such approaches viable in an increasing number of species.

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