The Physiology of Adventitious Roots[1]

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Adventitious roots are plant roots that form from any nonroot tissue and are produced both during normal development (crown roots on cereals and nodal roots on strawberry [Fragaria spp.]) and in response to stress conditions, such as flooding, nutrient deprivation, and wounding. They are important economically (for cuttings and food production), ecologically (environmental stress response), and for human existence (food production). To improve sustainable food production under environmentally extreme conditions, it is important to understand the adventitious root development of crops both in normal and stressed conditions. Therefore, understanding the regulation and physiology of adventitious root formation is critical for breeding programs. Recent work shows that different adventitious root types are regulated differently, and here, we propose clear definitions of these classes. We use three case studies to summarize the physiology of adventitious root development in response to flooding (case study 1), nutrient deficiency (case study 2), and wounding (case study 3).

ECONOMY, ECOLOGY, AND EXISTENCE

In plants, roots that form from nonroot tissues are known as adventitious roots. This general definition distinguishes adventitious roots from primary and lateral roots. However, there are subgroups of adventitious roots that can be formed as a stress response and during normal development. Figure 1 illustrates some examples of this diversity of adventitious root types, including but not restricted to junction roots; nodal roots (both crown and brace roots in monocots and nodal roots in eudicots such as strawberry [Fragaria spp.]); nonnodal prop or stem roots used for support (as in ivy and mangroves); stress-induced roots (Arabidopsis [Arabidopsis thaliana] etiolated hypocotyl, flooding, burial, and dark induced); and roots formed in response to soil chemicals (nutrient deficiency and heavy metals) or wounding (on cuttings).

Recent work has shown that many of these root types are differentially regulated (Hochholdinger et al., 2004; Atkinson et al., 2014; Bellini et al., 2014; Pacurar et al., 2014), and this likely impacts their function and physiology. As a result, we suggest that descriptions of adventitious roots be precise; to this end, we have composed Table I to provide clear descriptions, which include the conditions triggering each specific type of adventitious root development. For example, roots that form on stems in response to flooding are described as flood-induced stem roots; likewise, crown roots that form as a result of flooding are described as flood-induced crown roots. This scheme can be applied to most plant root systems and will help the plant community clarify differences among root types.

Economically, adventitious roots are very important. Propagation using cuttings is central to many forestry and horticulture industries, including the production of woody crops like apple (Malus domestica), grapes (Vitis vinifera), and stone fruit. In addition, cereal crops depend on a root system dominated by crown and brace roots.

Ecologically, adventitious roots are important for stabilizing shifting environments such as coastal regions (seagrasses; Ondiviela et al., 2014), estuaries, and river flood plains (Krauss et al., 2003). They are important for plant survival under abiotic and biotic stress conditions and are induced during flooding in a wide range of species (see case study 1). They are also important in response to other stresses, including heavy metals (for review, see Steffens, 2014), burial (Dech and Maun, 2006), drought (Liao et al., 2012), nutrient deficiencies (see case study 2), and biotic or abiotic wounding (Simberloff et al., 1978). This wound-induced adventitious rooting is the basis of cutting propagation (see case study 3).

In addition to the economic and ecological importance of adventitious roots, they play a key role for our existence. The cereal crops wheat (Triticum aestivum), rice (Oryza sativa), and maize (Zea mays) provide 60% of global caloric intake (Food and Agriculture Organisation of the United Nations). Cereal crops, like most monocots, rely on root systems composed almost exclusively of adventitious roots. If we are to achieve global food security, we need to improve food production in the face of increasing extreme weather events such as floods. In addition, we must do this more sustainably through reduced fertilizer applications. Adventitious roots have evolved to help plants tolerate a variety of stressful conditions, and understanding the importance of these adventitious root types in many crops will aid our development of nutrient-efficient and environmentally resilient crops.

To highlight the potential of exploiting adventitious roots for crop improvement, we now present three

Figure 1. Examples of adventitious root types. This figure highlights a few examples of the diversity of adventitious roots. A to D show types of adventitious roots that form during normal development, including those potentially established in the embryo (A); the dominant root system of monocots, including maize (top image) crown roots (yellow) and brace roots (orange) and nodal roots on other grasses (bottom image; B) and on eudicots such as strawberry (C); and nonnodal roots that provide support for plants such as ivy (top image) and mangroves (bottom image; D). E to H show adventitious root development under stressed conditions: Arabidopsis under low or no light (used as a model for adventitious root regulation; E); burial (top image) or flooding (bottom image) can induce adventitious roots from either nodal or nonnodal stem positions (F); nutrient or heavy metal stress increases adventitious root development (G); and wounding such as cutting induces de novo adventitious root development (H). Primary and seminal roots are depicted in white, first order lateral roots in blue, and second order lateral roots in pink.
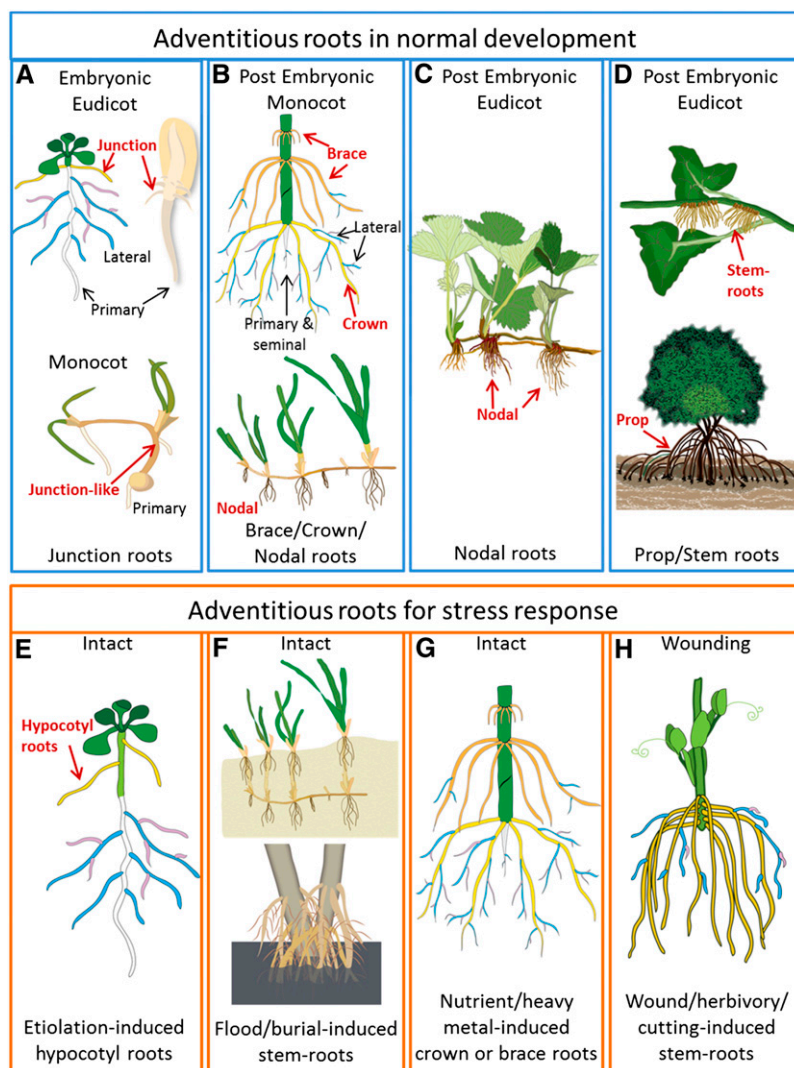
case studies of adventitious root physiology, focusing on responses to flooding, nutrient deficiency, and wounding.

CASE STUDY 1: FLOOD-INDUCED ADVENTITIOUS ROOTS

Flooding is a severe abiotic stress that is increasing in frequency worldwide (Brakenridge). One key aspect of flooding is the 10,000-fold slower diffusion rate of gases in water compared with that in air (Armstrong et al., 1991; Blom and Voesenek, 1996; Bailey-Serres and Voesenek, 2008), resulting in low oxygen availability and the trapping of gases in submerged tissues. Higher plants have evolved many metabolic and morphological adaptations to flooding (Bailey-Serres et al., 2012; Voesenek and Bailey-Serres, 2013; Abbas et al., 2015). A key response of many species, including rice (Lorbiecke and Sauter, 1999), *Rumex* spp. (Visser et al., 1996), tamarack (*Larix laricina*; Calvo-Polanco et al., 2012),

Eucalyptus spp. (Argus et al., 2015), and tomato (*Solanum lycopersicum*), is the emergence of adventitious roots.

In rice, bittersweet (*Solanum dulcamara*), and *Rumex palustris*, adventitious root primordia form during normal development and, upon flooding, can emerge as roots. In sunflower (*Helianthus annuus*), some tomato cultivars (Kramer, 1951; Negi et al., 2010; Dawood et al., 2014), and trees such as *Eucalyptus* spp. and tamarack, adventitious roots develop de novo upon flooding stress (Table II). Submergence-induced adventitious root growth is a complex process mediated by cell division in the root apical meristem and elongation of basal cells in root primordia (Lorbiecke and Sauter, 1999).

The timing of flood-induced adventitious root emergence is species specific (Lorbiecke and Sauter, 1999; Dawood et al., 2014; Argus et al., 2015) and depends on the developmental stage of the plant, the water temperature (Zhang et al., 2015) and depth (e.g. soil waterlogging, partial or complete submergence), and the flood duration (summarized in Table II). In rice,

Table I. *Adventitious root descriptions based on physical characteristics and induction conditions*

Parameter	Junction Roots	Hypocotyl Roots	Crown Roots	Brace Roots	Nodal Roots	Stem Roots	Prop Roots
Definition	Roots that form specifically at the root-shoot junction (e.g. Arabidopsis and bean)	Roots that form on the hypocotyl (e.g. bean and tomato)	Nodal roots that form below soil level as part of normal postembryonic development (e.g. rice, wheat, and maize)	Nodal roots that form above soil level as part of normal postembryonic development (e.g. maize)	Roots that form from nodes (e.g. strawberry and grass rhizomes)	Roots that form from internode (e.g. ivy)	Roots used for physical support (e.g. mangroves, where they also aid in aeration via lenticels and aerenchyma)
Induced by							
Flood		Flood-induced hypocotyl roots	Flood-induced crown roots	Flood-induced brace roots	Flood-induced nodal roots	Flood-induced stem roots	
Burial (including layering in propagation)					Burial-induced nodal roots	Burial-induced stem roots	
Etiolation		Etiolation-induced hypocotyl roots					
Wound						Wound-induced stem roots	Wound-induced prop roots
Heavy metals			Heavy-metal-induced crown roots	Heavy metal-induced brace roots	Heavy metal-induced nodal roots	Heavy metal-induced stem roots	
Nutrient			Nutrient-induced crown roots	Nutrient-induced brace roots	Nutrient-induced nodal roots		

root emergence also depends on the age and developmental stage of the respective node (Lorbiecke and Sauter, 1999; Steffens et al., 2012). At the third and fourth nodes, adventitious root emergence occurs earlier than at more apical nodes, because in older nodes,

almost all root primordia tips are in direct contact with the epidermis, while in younger nodes, parenchymal cells cover the root primordia (Steffens et al., 2012).

Adventitious roots facilitate gas transport and water and nutrient uptake during flooding. Following flooding,

Table II. *Comparison of adventitious root growth induced by flooding in some model species*

| Species	Adventitious Root Primordia	Adventitious Root Emergence	Reference
Poaceae			
Deepwater rice	Preformed at nodes	10 h after onset of partial submergence	Lorbiecke and Sauter (1999)
Asteraceae			
Sunflower	De novo upon flooding	2 d after onset of waterlogging	Wample and Reid (1978)
Solanaceae			
Bittersweet	Preformed at the main stem and branches	2 to 3 d after onset of partial submergence at 20°C or after 7 d at 13°C	Dawood et al. (2014); Zhang et al. (2015)
Tomato	Preformed or de novo upon flooding	1 d after onset of flooding at hypocotyls; 2 to 3 d after onset of flooding in 4-week-old plants	Vidoz et al. (2010)
Wetland species			
R. palustris	Preformed	2 d after onset of waterlogging	Visser et al. (1996)
Flood-tolerant trees			
E. camaldulensis ssp. *refulgens*	De novo upon flooding	5 d of waterlogging at seedling stage	Argus et al. (2015)
Tamarack	De novo upon flooding	Time unknown; analyzed after 6 months of flooding	Calvo-Polanco et al. (2012)

they help take up nutrients and ensure plant survival (Sauter, 2013). In the next sections, we summarize the signals and morphological changes involved in flood-induced adventitious root formation and growth in both monocots (e.g. rice) and eudicots (e.g. tomato).

Adventitious Root Growth Regulation upon Flooding

During submergence, ethylene biosynthesis increases in deepwater rice plants (Raskin and Kende, 1984a, 1984b; Kende et al., 1998), and because it is a gas, it also accumulates due to physical entrapment (Fig. 2; Musgrave et al., 1972). Ethylene is the major hormone that induces adventitious root growth in rice (Lorbiecke and Sauter, 1999) and tomato (Kim et al., 2008; Negi et al., 2010; Vidoz et al., 2010). The production of ethylene increases in submerged tomato plants due to enhanced ethylene biosynthesis via the rate-limiting enzyme 1-aminocyclopropane-1-carboxylic acid synthase (Vidoz et al., 2010). This increased ethylene promotes adventitious root formation through *NEVER-RIPE*

(*NR*; Kim et al., 2008; Negi et al., 2010; Vidoz et al., 2010), which encodes the ethylene receptor LeETR3 of subfamily I of the *LeETR1* to *LeETR6* gene family (Wilkinson et al., 1995). *NR*-deficient tomato plants are ethylene insensitive and exhibit a reduced number of adventitious roots either upon submergence or after ethylene treatment (Clark et al., 1999; Vidoz et al., 2010).

In rice, ethylene-mediated adventitious root development also requires signaling via auxin (Fig. 2; Zhou et al., 2003; Pacurar et al., 2014). Auxin is well known to regulate adventitious root development. In flooded rice plants, inhibitor studies using *N*-1-naphthylphthalamic acid indicate that polar auxin transport through the PIN-FORMED (PIN) family of auxin efflux carriers is required for adventitious root growth both in adult plants (B. Steffens, unpublished data) and in seedlings (Xu et al., 2005). *OsPIN1* RNA interference transgenic plants exhibit the same number of adventitious root primordia but show fewer emerged adventitious roots, indicating that PIN1 is involved in root emergence but not initiation (Xu et al., 2005). In addition, auxin
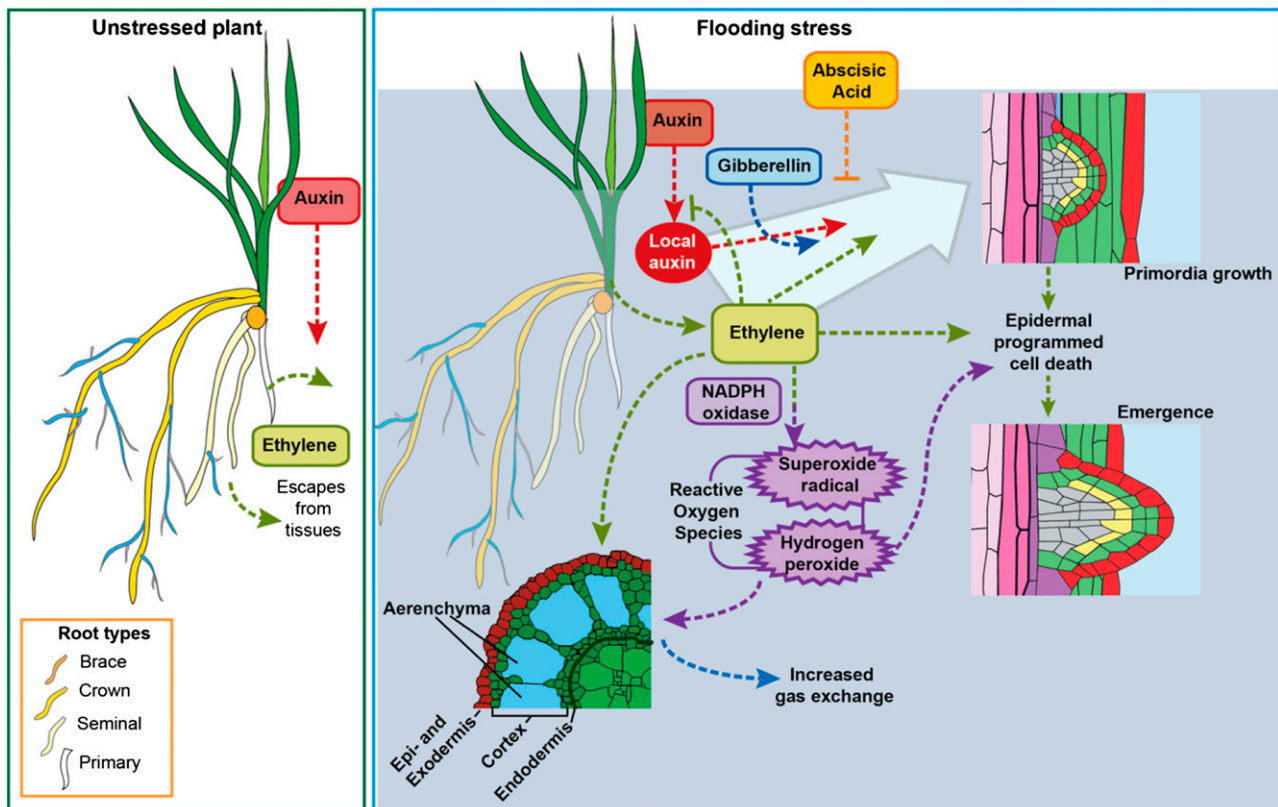
Figure 2. Adventitious root development in response to flooding. Under aerated conditions, gaseous ethylene escapes from plant tissues, but during flooding, water acts as a physical barrier, trapping ethylene in the plant. GA enhances the ethylene-promoted adventitious root growth, while abscisic acid reduces the effect. Ethylene triggers reactive oxygen species production, and together they trigger epidermal programmed cell death for root emergence and cortical programmed cell death lysigenous aerenchyma formation. The main difference in some eudicots (e.g. tomato) is the requirement for de novo adventitious root initiation via auxin and ethylene signaling. In the cross section, epidermis and exodermis are combined, but the exodermis can be several cell layers adjacent to the epidermis. Yellow roots are adventitious roots, blue and pink roots are lateral roots, and white roots are primary roots. Pointed arrows represent positive interactions, and flat-ended arrows represent negative interactions.

transport is a prerequisite for adventitious root development in tomato (Tyburski and Tretyn, 2004; Negi et al., 2010; Vidoz et al., 2010). Together with ethylene, auxin positively regulates adventitious root initiation through *DIAGEOTROPICA* (*DGT*; Vidoz et al., 2010; Lombardi-Crestana et al., 2012), which encodes SlCYP1, a cyclophilin A-type protein. SlCYP1 changes the abundance of auxin efflux carriers of the PIN family at the plasma membrane and, hence, modulates polar auxin transport (Oh et al., 2006; Ivanchenko et al., 2015; Retzer and Luschnig, 2015; Spiegelman et al., 2015). *dgt* mutant plants exhibited low sensitivity to auxin and inhibited submergence-induced ethylene biosynthesis, resulting in a reduced number of adventitious roots relative to the wild type (Vidoz et al., 2010).

In rice, the development of nodal adventitious root primordia requires the transcription factors CROWN ROOTLESS5 (CRL5) and ADVENTITIOUS ROOTLESS1 (ARL1 [also named CRL1]; Suge, 1985; Bleecker et al., 1986; Inukai et al., 2005; Liu et al., 2005). *CRL5* belongs to the APETALA2/ETHYLENE RESPONSE FACTOR gene family, and *ARL1* is an ethylene- and auxin-responsive gene that belongs to the ASYMMETRIC LEAVES2/LATERAL ORGAN BOUNDARIES domain gene family (Inukai et al., 2005; Liu et al., 2005). Both *CRL5* and *ARL1* are targets of transcription factors of the AUXIN RESPONSE FACTOR gene family, which link crown root development to auxin signaling (for review, see Sauter and Steffens, 2014).

Another class of hormones suggested to modulate polar auxin transport is the terpenoid lactone strigolactones (see case studies 2 and 3). However, the involvement of strigolactones in submergence-induced adventitious root development has yet to be determined.

Ethylene-induced adventitious root growth in adult rice plants upon flooding is mediated not only by hormonal signals but also by reactive oxygen species (Fig. 2; Steffens et al., 2012). Reactive oxygen species such as superoxide anion and hydrogen peroxide are created as a normal part of development, and antioxidant enzymes maintain normal homeostatic levels (for review, see Steffens, 2014). Superoxide anions are converted to hydrogen peroxide by superoxide dismutase and/or peroxidase enzymes (for review, see Steffens, 2014). Catalase then detoxifies hydrogen peroxide, which is involved in both signaling and programmed cell death. Under stress conditions, the amount of reactive oxygen species changes via either increased production of reactive oxygen species or changes in antioxidant levels (Bouranis et al., 2003; Steffens, 2014). In flooded rice plants, ethylene enhances superoxide anion generation by plasma membrane-located NADPH oxidase (Fig. 2). The accumulation of endogenous reactive oxygen species enhanced root growth through inhibition of the scavenging enzyme catalase (with aminotriazole), whereas hydrogen peroxide scavenging (with potassium iodide) inhibited this growth (Steffens et al., 2012), demonstrating the importance of hydrogen peroxide in crown root growth.

In rice, nodal adventitious root primordia never break through the epidermis without an exogenous trigger and internal ethylene accumulation (Steffens et al., 2006). When stimulated to grow, these nodal adventitious roots exert a mechanical force on the overlying epidermal cells, resulting in epidermal programmed cell death (Steffens et al., 2012). Epidermal programmed cell death above root primordia ensures that the tip of the growing root is not damaged during emergence (Mergemann and Sauter, 2000). Both epidermal programmed cell death and adventitious root growth are regulated through the interaction of ethylene, GA, and abscisic acid (Fig. 2; Steffens and Sauter, 2005; Steffens et al., 2006). GA promotes ethylene-triggered adventitious root growth (Suge, 1985; Lorbiecke and Sauter, 1999; Steffens et al., 2006), and abscisic acid inhibits both ethylene-induced and GA-promoted adventitious root emergence (Steffens et al., 2006). In adult *mhz4* mutant rice plants, a decreased abscisic acid level and an increased ethylene concentration resulted in enhanced adventitious root growth (Ma et al., 2014), supporting the idea that alterations in abscisic acid and ethylene concentrations are a prerequisite for adventitious root growth in rice. It is unknown whether adventitious root emergence in tomato is facilitated by cell wall loosening of stem tissue through expansins such as LeEXP1 (Rose et al., 2000) or by programmed cell death of covering epidermal cells, as was described for rice (Mergemann and Sauter, 2000; Steffens et al., 2012).

Flooded tamarack seedlings possess fewer but longer adventitious roots compared with seedlings grown in air (Calvo-Polanco et al., 2012). Interestingly, the endodermis of these longer adventitious roots is poorly developed, cell walls are less suberized, tracheids possess a smaller diameter, and cortex cells are filled with starch (Calvo-Polanco et al., 2012). Despite the reduced chlorophyll content in needles of flooded seedlings, photosynthesis and transpiration were not altered, suggesting that the morphological changes of these adventitious roots contribute to seedling survival. These nonwoody secondary roots may serve as sinks for carbohydrates, as perhaps indicated by the abundance of starch in cortex cells. This adaptive response is considered to be a typical mechanism of flooding-tolerant trees (Gravatt and Kirby, 1998).

Adventitious Root Aerenchyma Facilitate Gas Transport

Another type of morphological response to flooding is the production of air-filled aerenchyma (Fig. 2). Newly formed adventitious roots of many species develop aerenchyma in the root cortex together with an inducible barrier of thickened cell walls to prevent radial oxygen loss upon flooding (Drew et al., 1979; Colmer et al., 2006; Argus et al., 2015). Root aerenchyma connected to the shoot help to maintain the diffusion of gases and, hence, enable the plant to survive under flooded and oxygen-deficient conditions. Radial oxygen loss supports longitudinal gas transport

toward the apex, as demonstrated in roots of different deepwater, paddy, or upland rice varieties (Armstrong, 1971; Colmer, 2003).

In rice, aerenchyma formation in adventitious roots in stagnant water is induced within 12 h (Webb and Jackson, 1986) and results in a relatively high porosity of 30% to 40% depending on the genotype (Colmer, 2003). Ethylene mediates aerenchyma formation in adventitious roots but does not induce the barrier to radial oxygen loss (Colmer et al., 2006), indicating differential regulation of both processes.

Flood-tolerant trees also develop adventitious root aerenchyma upon flooding. In adventitious roots of soil-flooded *Eucalyptus camaldulensis* ssp. *refulgens* seedlings, root porosity increased about 14% in comparison with unflooded seedlings (Argus et al., 2015), indicating that the presence of aerenchyma upon flooding is an adaptive response of this riparian tree species. Aerenchyma formation was linked to flood tolerance in *Rumex* spp., with the more flood-tolerant *Rumex palustris* producing more aerenchyma than the less tolerant *Rumex acetosa* (Herzog and Pedersen, 2014).

CASE STUDY 2: ADVENTITIOUS ROOTS FOR IMPROVED NUTRIENT USE EFFICIENCY

Plants require a combination of three structural nutrients (carbon, hydrogen, and oxygen), six macronutrients (nitrogen, phosphorus, potassium, calcium, magnesium, and sulfur), and eight micronutrients (boron, chlorine, cobalt, copper, iron, manganese, molybdenum, and zinc; Timilsena et al., 2015). In most intensive farming situations, nutrients are added to the soil in the form of fertilizer. In 2010 to 2011, global application of nitrogen, phosphorus, and potassium totaled 104.1, 40.5 and 27.6 million tons, respectively (Timilsena et al., 2015). However, between 50% and 70% of nitrogen (for example) is lost through volatilization or runoff, polluting waterways through eutrophication (Robinson et al., 2011; Timilsena et al., 2015). Fertilizer production is also both energy and financially expensive, highlighting the importance of developing nutrient-efficient crops. To efficiently improve food production, we need an understanding of nutrient mobility in the rhizosphere and in the plant.

Responses to nutrient deficiencies begin with changes in deficiency-responsive genes, which then lead to physiological changes. There is less known about the deficiency-responsive genes in adventitious roots, and we recommend reviews on these genes in Arabidopsis and other model species (Atkinson et al., 2014; Bellini et al., 2014). Using cereals and the eudicot bean (*Phaseolus vulgaris*), the following section will focus on nutrient uptake by different adventitious roots and physiological responses to changing nutrient conditions.

Adventitious Root Responses to Nutrient Deficiency

Nutrient uptake occurs via transporters in the root (Fig. 3). Rice has 13 known phosphate transporters and an additional 13 putative transporters (Rose et al., 2013). Upon detection of low nutrient levels, the expression of these transporter genes increases to improve uptake capacity. For example, in rice crown roots, low potassium (Chen et al., 2015) or zinc (Widodo et al., 2010) increases expression of the potassium (OsHAK1 and OsHAK5; Chen et al., 2015) or zinc (ZIP family; Widodo et al., 2010) transporters, respectively, and maize nitrogen transporter gene expression increases in different root types under low-nitrogen conditions (Yu et al., 2014).

Perhaps surprisingly, there are differences in nutrient uptake ability among different types of roots (Table III). For example, using labeled uptake studies, under high-nitrogen (maize) or high-sulfur (rice) conditions, primary roots show greater nitrogen uptake than seminal roots (embryonic roots that emerge adjacent to the radicle; Fig. 3). The crown roots had the lowest nitrogen uptake (although the crown root measurements for the nitrogen study were done in plants different in age from those used for the primary and seminal measurements; Maniou et al., 2014; Yu et al., 2014). For low-nitrogen conditions, crown root uptake is reduced less (Yu et al., 2014), whereas for sulfur, the percentage reduction was similar for each root type (except for mesocotyl roots, which are similar to hypocotyl roots in monocots and had a much bigger reduction in sulfate uptake; Maniou et al., 2014). In wheat plants grown in aerated conditions, phosphorus uptake was initially higher in seminal roots than in crown roots, but this trend reversed in slightly older plants (Wiengweera and Greenway, 2004). However, in stagnant, flooded conditions, crown roots showed consistently higher phosphorus and potassium uptake than did seminal roots (Wiengweera and Greenway, 2004). This trend was also found in the eudicot bean, in which basal roots (i.e. roots at the base of the bean hypocotyl) had higher phosphate uptake under low phosphorus (Rubio et al., 2004).

When maize roots are exposed to patchy nutrient conditions, nutrient uptake responds differently for each root type. This is summarized in the lower part of Table III (Yu et al., 2014). For example, crown roots take up more ^{15}N under homogenous low-nitrogen conditions than they do under homogenous high nitrogen, a trend that is reversed for primary and seminal roots (Yu et al., 2014). However, both primary and crown roots have the highest uptake of nitrogen when that root type is exposed to local high nitrogen, whereas seminal roots had the highest uptake under locally low levels of nitrogen (Yu et al., 2014). These findings demonstrate significant physiological differences between each root type.

Root Architecture Response to Nutrient Deficiency

Each root type forms in different vertical positions, exposing them to different layers of the soil. Because nutrients are not evenly distributed in the soil, changes in root architecture can change the efficiency of nutrient uptake. For example, phosphorus is more available in
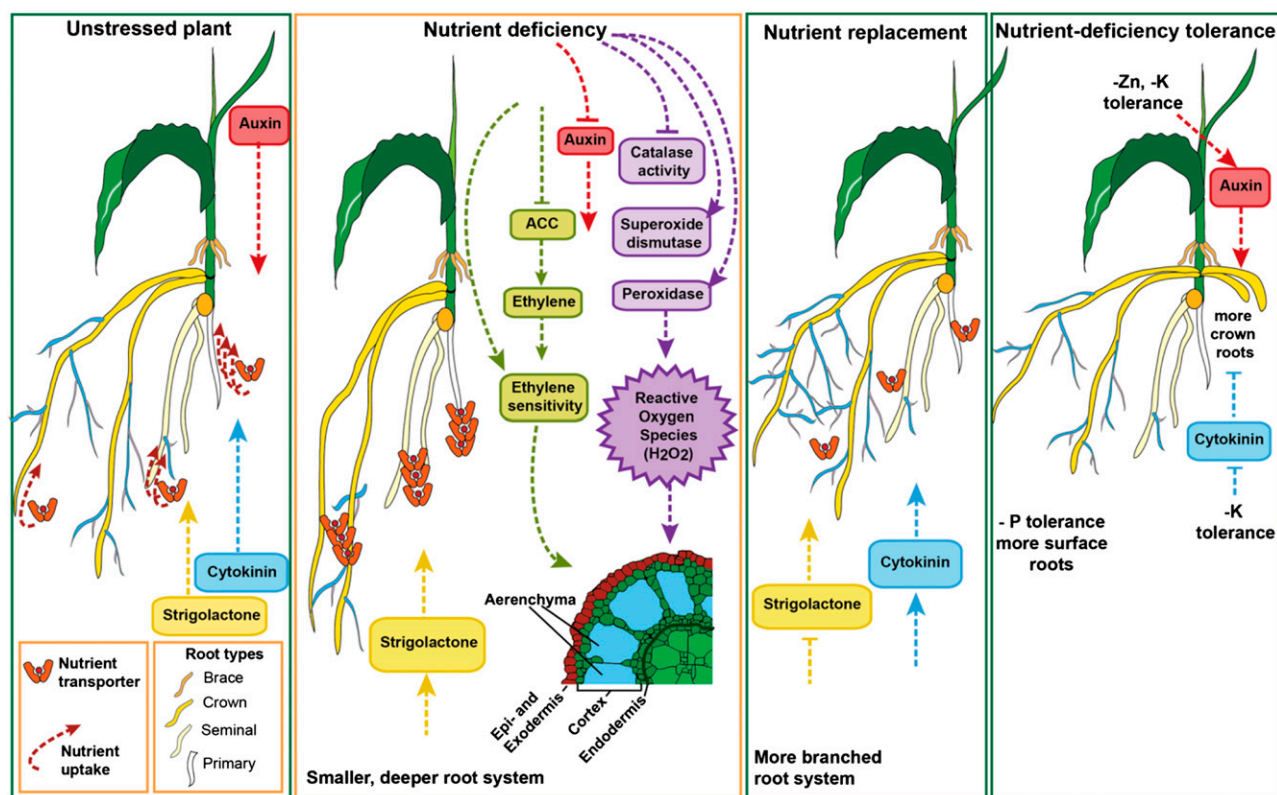
Figure 3. Nutrient responses in adventitious roots. Under nutrient-replete conditions, crown roots have the lowest nutrient uptake rates, followed by seminal roots, while the primary roots have the highest uptake. When nutrients are deficient, the expression of nutrient transporters increases. In addition, strigolactone increases while auxin decreases, resulting in long roots with minimal lateral roots. Reactive oxygen species increase via changes in antioxidant enzyme activity (catalase, superoxide dismutase, and peroxidase) and, together with enhanced ethylene sensitivity, trigger lysigenous aerenchyma formation. When nutrients are replaced, nutrient transporter expression decreases systemically, cytokinin production increases, strigolactone levels decrease, and lateral root initiation increases on the adventitious roots. In potassium and zinc deficiency-tolerant lines, auxin signaling increases, and in potassium-efficient lines, cytokinin signaling decreases, together resulting in more adventitious roots. In phosphorus-efficient lines, more adventitious roots are found in the surface layers of the soil. In the cross section, epidermis and exodermis are combined, but the exodermis can be several cell layers adjacent to the epidermis. Pointed arrows represent positive interactions, and flat-ended arrows represent negative interactions. –K, Potassium deficiency; –P, phosphorus deficiency; –Zn = zinc deficiency. Yellow roots are crown roots, orange roots (the upper, short ones here) are brace roots (both adventitious root types), cream roots are seminal roots, white roots are primary roots, and blue and pink roots are lateral roots. ACC, 1-Amino-cyclopropane-1-carboxylic acid (an ethylene precursor).

the 10- to 15-cm depth (Miller et al., 2003), so increased tolerance to phosphorus-deficient soils may be a result of having more surface roots (Fig. 3). Phosphorus-efficient bean lines grew more adventitious roots (either stem or basal roots) in the surface soil layers, whereas less efficient lines either increased the number of deeper roots or failed to respond to phosphorus deficiency (Bonser et al., 1996; Liao et al., 2001; Miller et al., 2003; Miguel et al., 2013). This was also the case in pea (*Pisum sativum*) and soybean (*Glycine max*; Bonser et al., 1996).

Furthermore, the root system response is systemic, such that if any root is exposed to high phosphorus, the root system as a whole responded as if it were exposed to uniform high phosphorus (Bonser et al., 1996). Increases in phosphorus uptake with shallower roots also corresponded with increased yield in bean

(Bonser et al., 1996; Liao et al., 2001; Richardson et al., 2011), so improvements in phosphorus efficiency could be achieved by selecting shallower root systems. However, the tradeoff with shallow roots is a reduction in drought tolerance because the deeper soil layers contain more water, so the ideal scenario for tolerating drought and phosphorus deficiency is a combination of deep and shallow roots (Uga et al., 2011, 2012; Rose et al., 2013). Recent identification of quantitative trait loci for both shallow and deep rooting in rice (Uga et al., 2011, 2012) and bean (Liao et al., 2004; Richardson et al., 2011) suggest that this may be a real possibility (Rose et al., 2013).

The growth and response of adventitious roots vary between nutrients and between tolerant and intolerant varieties. For example, zinc deficiency reduces the number of crown roots by up to 75% in a sensitive rice

Table III. Trends in nutrient uptake of different root types of monocot species

Growth Condition	Nutrient Measured	Trends for Monocot Root Type Uptake	Species/Reference
Replete nitrogen	Nitrogen	Primary > seminal > > crown	Maize/Yu et al. (2014)
Low nitrogen	Nitrogen	Primary > crown > seminal	Maize/Yu et al. (2014)
Replete sulfur	Sulfur	Primary > seminal > mesocotyl > crown	Rice/Maniou et al. (2014)
Low sulfur	Sulfur	Seminal > primary > mesocotyl > crown	Rice/Maniou et al. (2014)
Replete sulfur	Sulfate	Seminal > mesocotyl > primary > crown	Rice/Maniou et al. (2014)
Low sulfur	Sulfate	Seminal > primary > crown > mesocotyl	Rice/Maniou et al. (2014)
Aerated	Phosphorus	Seminal > crown (reversed over time)	Wheat/Wiengweera and Greenway (2004)
Stagnant	Phosphorus	Crown > seminal (all times measured)	Wheat/Wiengweera and Greenway (2004)
Aerated	Potassium	Crown > seminal (all times measured)	Wheat/Wiengweera and Greenway (2004)
Stagnant	Potassium	Crown > seminal (all times measured)	Wheat/Wiengweera and Greenway (2004)
Root type		Trends for nitrogen (N) uptake (Yu et al., 2014)	
Primary		Local high N > homogenous high N > local low N > homogenous low N (60% reduction)	
Seminal		Local low N > homogenous high N > local high N > homogenous low N (71% reduction)	
Crown		Local high N > homogenous low N > homogenous high N > local low N (86% reduction)	

cultivar, whereas crown root number is maintained in a tolerant cultivar, a trait shared by many tolerant cultivars (Widodo et al., 2010; Rose et al., 2013).

Work has begun on improving tolerance to nutrient-deficient conditions by introducing genes linked to changes in root architecture, such as *PHOSPHORUS-STARVATION TOLERANCE1* (*PSTOL1*; Gamuyao et al., 2012) or the WUSCHEL-related homeobox gene *OsWOX11* (Chen et al., 2015). PSTOL1 is a phosphorus deficiency-tolerant protein kinase found in the *aus*-type rice varieties but not in all other types (Gamuyao et al., 2012). The OsWOX11 lines have used a potassium deficiency-induced gene promotor that drives the expression of *OsWOX11* (Chen et al., 2015). The OsWOX11 and PSTOL1 rice varieties produced bigger root systems than the wild types under low potassium (Chen et al., 2015) and phosphorus (Gamuyao et al., 2012), respectively. These larger root systems also showed improved uptake of other nutrients (Gamuyao et al., 2012; Chen et al., 2015), resulting in higher yield (Chen et al., 2015). These two examples demonstrate that manipulating the adventitious root system can benefit the uptake of more than just that single nutrient. *PSTOL1* expression correlates with the expression of *ARL1/CRL1* and *RR2* (a cytokinin type A response regulator), suggesting that changes in architecture could be linked to these networks (Gamuyao et al., 2012). Interestingly, *PSTOL1* expression is present in primordia of crown roots but not in seminal roots (Gamuyao et al., 2012), highlighting differences in root types.

Not only do root types differ in the number of roots produced and their growth response to different nutrient deficiencies, but they also differ in the number of lateral roots that form on each root type. In rice, phosphate or nitrate deficiency results in longer roots with fewer lateral roots on the seminal roots (Rose et al., 2013; Sun et al., 2014), whereas zinc deficiency reduced the number on crown roots but had little effect on root length (Widodo et al., 2010). Using split-root experiments, Yu et al. (2014, 2015) demonstrated that, although lateral root density increased on maize crown roots that were exposed to locally high concentrations of nitrate, lateral root density was not affected on seminal roots (Yu et al., 2014). This difference in lateral root initiation between seminal and crown roots further highlights the complex differences between the different root classes in maize.

Lateral root density also increased on adventitious roots of phosphorus-efficient bean lines (Miller et al., 2003). Low phosphorus increased the distance from the root tip to the first lateral root in adventitious roots, but in basal roots there was no change except in one inefficient line (Miller et al., 2003), again demonstrating differences between adventitious root types.

Nutrient Changes Alter Hormone Signaling in Adventitious Roots

Root induction is dependent on the interaction of different hormone networks (for a summary comparing adventitious and lateral roots, see Atkinson et al. [2014] and Bellini et al. [2014]). Generally, auxin promotes adventitious (and lateral) root initiation and decreases elongation, whereas cytokinin and strigolactones inhibit root initiation. Strigolactone levels increase systemically under low-phosphorus or low-nitrogen conditions in monocots, including rice and sorghum (*Sorghum bicolor*; Fig. 3; Yoneyama et al., 2007, 2015; López-Ráez et al., 2008; Umehara, 2011; Sun et al., 2014), and in dicots, such as pea and tomato (López-Ráez et al., 2008; Balzergue et al., 2011; Kohlen et al., 2012). Nitrogen and phosphorus deficiency responses were lost in the rice strigolactone mutants (Sun et al., 2014), demonstrating the importance of the strigolactone signaling pathway for nutrient responses in monocot roots (Umehara, 2011). However, the exact nature of the interaction between low nutrients, increased strigolactones, and changes in root architecture is not well understood (Rasmussen et al., 2013).

Because nutrient efficiency is linked to changes in root architecture, and because root architecture is regulated by signaling molecules, it is perhaps not surprising that tolerance of nutrient deficiency can

result from changes in hormone signaling (Fig. 3). For example, in rice, zinc deficiency-tolerant lines and the potassium-induced *WOX11* lines have increased expression of genes linked to auxin signaling compared with the intolerant line (Widodo et al., 2010; Chen et al., 2015). Furthermore, *WOX11* rice lines had reduced cytokinin signaling (Chen et al., 2015). The combination of down-regulating cytokinin signaling while up-regulating auxin signaling may explain the increase in adventitious root number and growth in these nutrient-efficient rice lines.

Lateral root induction also relies on changes in hormone signaling. Lateral root induction in maize crown roots exposed to local nitrogen patches occurs via a nitrate-induced increase in auxin levels. This includes increased expression of the monocot-specific *PIN9* followed by cell cycle induction in the phloem pole pericycle cells (Yu et al., 2015). The presence of monocot-specific PIN transporters involved in crown root developmental patterns supports the idea that they have evolved separately or divergently to control features of monocot-specific morphogenesis such as adventitious root development (Yu et al., 2015).

Nutrient Deficiency-Induced Aerenchyma

In addition to flooding (see case study 1), many nutrient deficiencies, including phosphorus (Drew et al., 1989; He et al., 1992; Siyiannis et al., 2012; Rose et al., 2013; Fu et al., 2014; Hu et al., 2014), nitrogen (Drew et al., 1989; He et al., 1992; Siyiannis et al., 2012), and sulfur (Bouranis et al., 2003; Siyiannis et al., 2012; Maniou et al., 2014), have been shown to induce root aerenchyma formation. This induction varies in speed of onset and severity depending on the specific nutrient deficiency. For example, in maize, nitrogen deficiency caused the fastest production of aerenchyma followed by sulfur; the least production was caused by phosphorus (Drew et al., 1989; Siyiannis et al., 2012), although the final percentage of aerenchyma was similar between both nitrogen and phosphorus deficiency (Drew et al., 1989).

Lysigenous aerenchyma forms through the lysis of cortical cells and helps improve the movement of gasses (Maniou et al., 2014), initiating in the center of the cortex (Bouranis et al., 2003). The spaces increase in size, leaving bridges of intact cells linking the epidermal layers to the endodermis. Similar to aerenchyma formation in flooded conditions, nutrient deficiency-induced aerenchyma formation depends on ethylene signaling (He et al., 1992). However, in contrast to during and following flooding, ethylene production decreases under nitrogen- or phosphorus-deficient conditions (Drew et al., 1989) but sensitivity to ethylene is increased (He et al., 1992). After the inductive ethylene signal (Fig. 3), cellulase activity peaks (Siyiannis et al., 2012), probably leading to the controlled destruction of cortical cells. In nitrogen-deprived roots, this peak in cellulase activity was earlier and higher than in phosphorus-deficient roots (Siyiannis et al., 2012), corresponding to the faster production of aerenchyma under nitrogen-deficient conditions.

In addition to changes in ethylene signaling, nutrient stress increases the production of reactive oxygen species (Bouranis et al., 2003; Fu et al., 2014). A deficiency of phosphorus (Fu et al., 2014) or sulfur (Bouranis et al., 2003) leads to increased levels of superoxide anion and hydrogen peroxide in crown roots of maize (Bouranis et al., 2003) and rice (Fu et al., 2014). In flooded conditions, hydrogen peroxide is known to be involved in programmed cell death (for review, see Quan et al., 2008), and in sulfur-deficient maize, superoxide anions and hydrogen peroxide were found in the degenerating cells of the root cortex (Bouranis et al., 2003) where aerenchyma form (Fig. 3). Changes in reactive oxygen species levels and peroxidase activity also increase lignification (Quan et al., 2008), which occurs in the exodermis, sclerenchyma (Fu et al., 2014), and endodermis (Bouranis et al., 2003) under phosphorus or sulfur deficiency (Fu et al., 2014). This potentially stabilizes the remaining cells, avoiding complete tissue collapse. Concurrent with the formation of aerenchyma, root porosity increased, resulting in higher levels of oxygen and hydrogen peroxide released from the roots (Fu et al., 2014).

CASE STUDY 3: WOUND-INDUCED ADVENTITIOUS ROOTS: CUTTING PROPAGATION

Wound-induced adventitious roots are central to the propagation of forestry and horticultural species, and recent work has begun to unravel the molecular and physiological steps leading to rooting. We focus here on the physiology of adventitious root initiation and emergence, including the wound response and the networks regulating adventitious root induction (summarized in Fig. 4).

Wound Response

Immediately after cutting, wound response signaling pathways are initiated at the base of the cutting (Creelman et al., 1992; Schilmiller and Howe, 2005), with a fast increase in jasmonic acid levels peaking 30 min after cutting (Fig. 4; Ahkami et al., 2009; Rasmussen et al., 2015). The presence of this peak correlated with adventitious root formation (Ahkami et al., 2009; Fattorini et al., 2009; Rasmussen et al., 2015), and a short pulse of jasmonic acid increased adventitious root formation (Rasmussen et al., 2015). However, in *Bupleurum kaoi* cuttings and intact Arabidopsis hypocotyls, prolonged exposure to jasmonic acid inhibited adventitious root formation (Chen et al., 2007; Gutierrez et al., 2012). In natural conditions, this wound response may be triggered by herbivory, physical damage, disease, or parasites (Schilmiller and Howe, 2005; Wasternack et al., 2006; Wasternack and Hause, 2013).
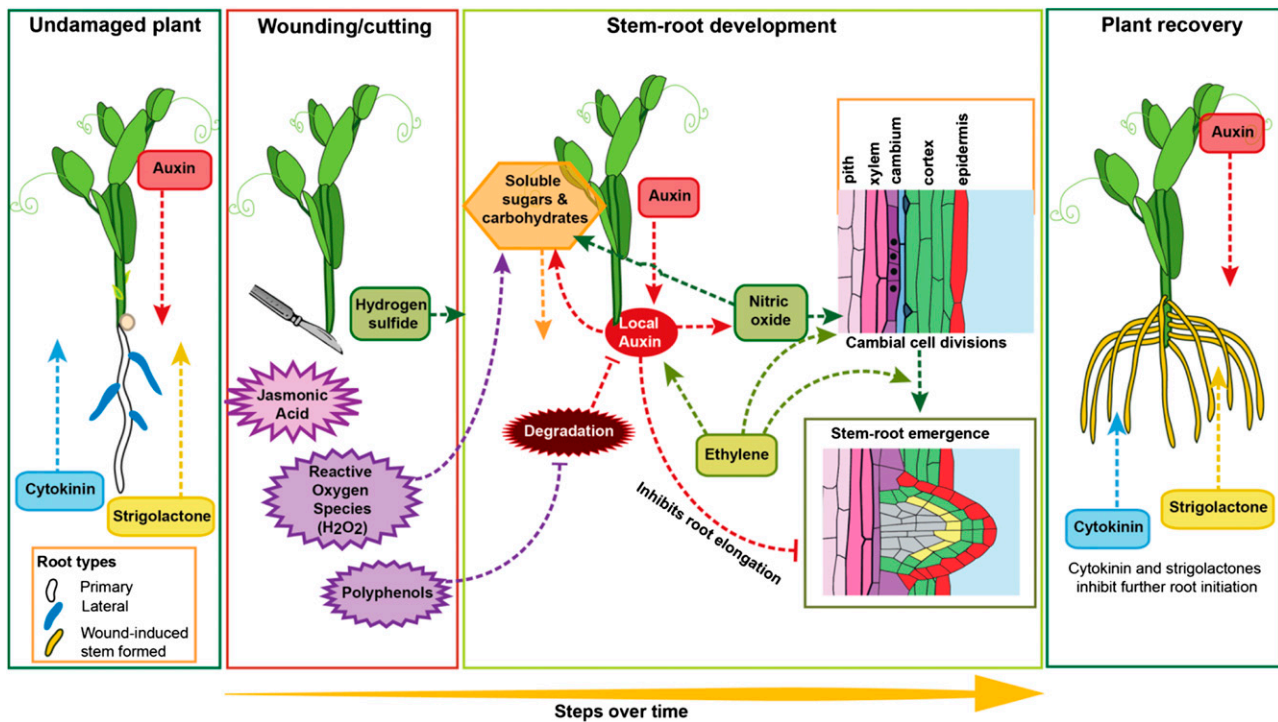
Figure 4. Adventitious root formation on cuttings. In intact plants, cytokinin and strigolactones are predominantly produced in the root, while auxin is predominantly produced in the shoot. On wounding, jasmonic acid peaks within 30 min and is required for successful root development. Reactive oxygen species, polyphenols, and hydrogen sulfide also increase and promote adventitious rooting. Polyphenols do this via reducing auxin degradation. Auxin builds up in the base of the cutting, acting upstream of nitric oxide to promote adventitious root initiation. Auxin, nitric oxide, and hydrogen peroxide (H_2O_2) increase soluble sugars, which can be used for root development. Furthermore, levels of root initiation inhibitors (cytokinin and strigolactone) are reduced with the removal of the original root system. At later stages, auxin inhibits primordia elongation while ethylene promotes adventitious root emergence. As the new root system establishes, the production of cytokinin and strigolactones is restored. Pointed arrows represent positive interactions, and flat-ended arrows represent negative interactions. Yellow roots are adventitious roots, the white root is a primary roots, and blue roots are lateral roots.

Similar to other stresses, including flooding and nutrient deficiency, physical damage also increases the production of reactive oxygen species (Fig. 4; Wasternack et al., 2006). Hydrogen peroxide is important for the wound response (Quan et al., 2008), as it increases adventitious root formation (Li et al., 2009; Santos Macedo et al., 2009; Li and Xue, 2010; Liao et al., 2010; She et al., 2010) via diamine oxidases (She et al., 2010). By contrast, catalase and ascorbic acid, which reduce hydrogen peroxide levels, both inhibited adventitious rooting (Li et al., 2009). Furthermore, the reduction in adventitious rooting that occurs by reducing auxin signaling (see below) can be partially rescued by treatment with hydrogen peroxide (Li et al., 2009). Hydrogen peroxide production begins to increase from 12 h after cutting and can reach seven times higher after 36 h (Li et al., 2009). Indole-3-butyric acid also increased hydrogen peroxide production (Li et al., 2009), suggesting feedback loops between auxin biosynthesis and signaling and reactive oxygen species signaling.

Because phenolic compounds help protect against reactive oxygen species (Jaleel et al., 2009), it is not surprising that they also increase in response to wounding. De Klerk and others (2011) tested a wide range of polyphenols and found that all of them promoted adventitious rooting, with ferulic acid having the strongest effect.

Adventitious Root Initiation

Adventitious root induction is promoted by high auxin and low cytokinin levels (Fig. 4; Bollmark and Eliasson, 1986; Bollmark et al., 1988; De Klerk et al., 1999; Kuroha et al., 2002, 2005). Auxin levels peak early after cutting in petunia (*Petunia hybrida*) and pea (Ahkami et al., 2013; Rasmussen et al., 2015) and then decrease, while cytokinin levels rapidly plummet with the removal of roots and then begin to recover at later stages (Bollmark et al., 1988; Rasmussen et al., 2015).

Auxin levels can be regulated by biosynthesis, transport, conjugation, and degradation. Reductions in any of these also alter adventitious rooting (Ahkami et al., 2013; da Costa et al., 2013). Auxin transport inhibitors significantly reduce adventitious rooting (Garrido et al., 1998, 2002; Koukourikou-Petridou, 1998;

Ford et al., 2001). More recently, however, it has been suggested that auxin degradation may also be responsible for changes in the rooting ability of pea or *Prunus* spp. cuttings (Liao et al., 2010; De Klerk et al., 2011; Osterc and Štampar, 2011; Rasmussen et al., 2015). De Klerk and others (2011) found that, at optimal concentrations of many of the phenolics tested, auxin degradation by decarboxylation was almost completely blocked, resulting in higher active auxin levels (Fig. 4). This protective role of auxin may explain the improvement in adventitious rooting with phenolic applications.

In addition to auxin and cytokinin, strigolactones also regulate adventitious root initiation (Kohlen et al., 2012; Rasmussen et al., 2012b). Strigolactones are produced predominantly in the roots (Gomez-Roldan et al., 2008; Umehara et al., 2008), so the main strigolactone source has been removed in cuttings. Shoot removal by decapitation (which is often used in cutting propagation) also reduces strigolactone levels (Gomez-Roldan et al., 2008; Umehara et al., 2008). Inhibition of strigolactones using mutants or chemical inhibitors improved the adventitious rooting of pea and tomato cuttings (Kohlen et al., 2012; Rasmussen et al., 2012a, 2012b), and strigolactones act independently of cytokinins in intact Arabidopsis hypocotyls (Rasmussen et al., 2012b). Strigolactones may act by altering auxin transport (Bennett et al., 2006; Rasmussen et al., 2012b); however, an independent role for strigolactones on adventitious rooting cannot be fully ruled out (Rasmussen et al., 2012b).

The effect of ethylene on adventitious rooting under nonwaterlogged conditions has been shown to be contradictory. For example, in tobacco (*Nicotiana tabacum*; McDonald and Visser, 2003), sunflower (Liu et al., 1990), and *Prunus avium* (Biondi et al., 1990), ethylene treatments reduced adventitious rooting. By contrast, the ethylene precursor 1-aminocyclopropane-1-carboxylic acid enhanced adventitious rooting in stem cuttings of grape (Riov and Yang, 1989) and Norway spruce (*Picea abies*; Bollmark and Eliasson, 1990), whereas ethylene appeared to have no effect on adventitious rooting in apple (Harbage and Stimart, 1996). Adding even more complexity, at high auxin levels, ethylene is inhibitory in mung bean (*Vigna radiata*) and *Eucalyptus* spp. (De Klerk and Hanecakova, 2008; Kilkenny et al., 2012), but at low auxin levels, ethylene promoted adventitious rooting in mung bean (De Klerk and Hanecakova, 2008). Ethylene is known to interact with both auxin (Růzicka et al., 2007; Lewis et al., 2011) and cytokinin (Bollmark and Eliasson, 1990; Ramírez-Carvajal et al., 2009), but the precise nature of this interaction in cutting propagation requires further study.

Nitric oxide and hydrogen sulfide increase adventitious rooting in a wide range of species (Fig. 4; Zhang et al., 2009; Li and Xue, 2010; Liao et al., 2010; Li et al., 2011). Zhang and others (2009) showed that hydrogen sulfide is produced 24 h after cutting, followed by auxin, followed by nitric oxide. Nitric oxide mediates the auxin response leading to adventitious root formation (Pagnussat et al., 2003, 2004; Zhang et al., 2009), and using treatments and inhibitors, it has been demonstrated that auxin acts upstream of nitric oxide (Zhang et al., 2009).

Aside from hormonal signals, resource availability is also an important factor in adventitious root formation on cuttings (Fig. 4; da Costa et al., 2013). During adventitious root development in teak (*Tectona grandis*) cuttings, the soluble sugar and starch levels decreased (Jasik and Klerk, 1997; Husen and Pal, 2007). Higher levels of soluble sugars improve adventitious rooting and survival in many species, including petunia (Druege and Kadner, 2008), *Pelargonium* spp. (Druege et al., 2004), *Chrysanthemum* spp. (Druege et al., 2000), and *Eucalyptus* spp. (Hoad and Leakey, 1996). Auxin (Jasik and Klerk, 1997; Husen and Pal, 2007), nitric oxide, and hydrogen peroxide (Liao et al., 2010) treatments increase total soluble sugar levels. Furthermore, it has been demonstrated that increased rooting of cuttings kept in low light can be linked to an increase in soluble sugar (Druege et al., 2004; Druege and Kadner, 2008; Husen, 2008; Klopotek et al., 2010).

These signaling pathways control the cell division and differentiation that leads to a new root primordium. In many species, adventitious roots form from cambial cell divisions, which either develop directly into a new primordium or first divide into a callus tissue before tracheid differentiation and primordia establishment (Bollmark et al., 1988; Kevers et al., 1997; De Klerk et al., 1999; Naija et al., 2009; Rasmussen et al., 2009; Rasmussen and Hunt, 2010). As the root tissues form, hormone signaling changes with the restoration of higher strigolactone and cytokinin production, possibly preventing uncontrolled cell division and root initiation. At these later stages of root development, the hormone signaling requirements also change, with auxin inhibiting root elongation (Kevers et al., 1997; De Klerk et al., 1999; da Costa et al., 2013) and cytokinin (Bollmark and Eliasson, 1986) and ethylene enhancing adventitious root emergence and elongation.

CONCLUSION

Clear evidence is emerging demonstrating that each type of adventitious root is regulated and responds to environmental cues in unique ways. Because adventitious roots are important for tolerance to stresses such as flooding, nutrient deficiency, and wounding in both monocot and eudicot species, it is important that we understand the commonalities and differences among these important root types.

In each of the case studies, the timing of both hormonal interaction and reactive oxygen species homeostasis is very important. In addition, a core signaling network regulates root initiation and emergence, with auxin and ethylene promoting and cytokinin and strigolactones inhibiting. The formation of aerenchyma in adventitious roots is common to both flooding and nutrient deficiency and reduces the energy requirement

for growth and maintenance. In flooded plants, aerenchyma is also crucial for enhancing gas exchange in this low-oxygen environment. Under nutrient deficiency, being able to adapt root architecture enables maximum nutrient capture, improving plant survival and crop yield. By manipulating recently identified nutrient transporters and quantitative trait loci for root angle, we now have the potential to improve breeding programs for nutrient-efficient crop lines. In future studies with combined stresses, this will prove extremely important. When flooding was combined with nutrient uptake studies, it was found that the adventitious roots had higher nutrient uptake ability compared with other root types (see case study 2). This could mean that nutrient-efficient lines, depending on surface adventitious roots, may also have improved flood tolerance. However, much more work is still required.

In summary, we have precisely defined and described the different adventitious root types and their physiological responses in particular to three stress conditions. Understanding the functional similarities and differences shared by these advantageous adventitious roots is crucial for maximizing efficient and resilient crop production.

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