Environmental, Developmental and Genetic Factors Controlling Root System Architecture

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A better understanding of the development and architecture of roots is essential to develop strategies to increase crop yield and optimize agricultural land use. Roots control nutrient and water uptake, provide anchoring and mechanical support and can serve as important storage organs. Root growth and development is under tight genetic control and modulated by developmental cues including plant hormones and the environment. This review focuses on root architecture and its diversity and the role of environment, nutrient and water as well as plant hormones and their interactions in shaping root architecture.

Introduction

The green revolution brought dramatic increases in food production through the development of high yielding, dwarf varieties of rice and wheat and the application of large quantities of inorganic fertilizer, pesticides, and irrigation water. Unfortunately, this increased agricultural production has had a deleterious environmental impact increasing soil salinity, depleting and polluting water resources and using ~8 % world oil output. In addition, the world population is estimated to reach ~8.3 Bn by 2030 with the majority of that increase occurring in the developing world (Royal Society, 2009). The need to feed this growing population sustainably, and avoiding the significant threats to food crop harvests arising from climate change, could not be more pressing. With no more agricultural land available, increases in

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food production of between 40-50% must be achieved through a sustainable intensification of agriculture over the next two decades (Royal Society, 2009).

The challenge of increasing crop production both with lower inputs of water and fertilizer as well as lower outputs in terms of greenhouse gas emissions is a significant one that will not be achieved without the translation of decades of basic research into plant biology. We know, for example, that root systems are central to the acquisition of water and nutrients by plants: Root system architecture (RSA) at both macro-scale (root length, branching and growth angle) and micro-scale (root diameter and root hair production) determines the distribution of root surface area within the soil profile and so the plant's capacity to capture nutrients and water (Lynch, 1995; Beaudoin *et al*., 2000; Hue *et al*., 2010; Osmont *et al*., 2007; Hochholdinger and Tuberosa, 2009, Coudert *et al*., 2010, Gewin, 2010; Atkinson *et al*., 2014). These traits therefore have a direct bearing on crop productivity, particularly under conditions of low resource availability (Lynch, 2007).

During recent years, the impact of the 'hidden half' on plant growth has become apparent in model systems such as Arabidopsis (*Arabidopsis thaliana*) and more importantly in crops like wheat (*Triticum aestivum*), rice (*Oryza sativa*), maize (*Zea mays*) and legumes (Goh *et al*., 2014; Bao *et al*., 2014; Herder *et al*., 2010; Coudert *et al*., 2010; Hochholdinger *et al*., 2004; De dorlodot *et al*., 2007). This review focuses on key factors influencing root system architecture.

Roots – structure and diversity of form

Roots have been defined as "axial multicellular structures of sporophytes of vascular plants which usually occur underground, have strictly apical elongation growth, and generally have gravitropic responses which range from positive gravitropism to diagravitropism, combined with negative phototropism" (Raven and Edwards, 2001; Sánchez-Calderón *et al*., 2013). Roots are essential for uptake of water and micro and macronutrients and also are the site of anchorage and constitute important storage organs. They additionally have a role in producing growth regulators that can be transported to the shoot and secondary metabolites such as flavonoids and alkaloids that can be involved in the defense against pathogens or in the cross talk with symbiotic microorganisms (Lynch and Brown, 2012; Montiel *et al*., 2004). Despite the importance of these organs there is still limited understanding of the mechanistic

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processes involved in many root functions. The root system results from the coordinated control of both genetic endogenous programs involving hormones and other developmental cues (regulating growth and organogenesis) and interactions with the soil and abiotic and biotic environmental stimuli (Hodge *et al.,* 2009). The root system of most 'higher' plants can be classified into three types of roots, the primary, lateral and adventitious (Fitter, 1991). The main root axes elongate deeply into the soil providing the initial framework from which the whole root system can be developed. However the lateral roots, which can in some cases occupy more than 90% of the total length of the whole root system, eventually play the major role in water and nutrient uptake (Chaves *et al.*, 2003; Horii *et al.*, 2006).

Root systems can be classified according to branch structure, root activity or development. The classification based on development is the more useful to analyze the root system growth. This approach has been used to classify roots into three categories: primary root (PR), lateral roots (LR) and adventitious roots (shoot-borne root). This classification reflects the differences between monocotyledonous and dicotyledonous root system (Atkinson *et al.*, 2014). Angiosperms have two main root system morphologies: allorhizic root system in dicots such as Arabidopsis, tomato and pea and homorhizic root system in monocots.

The allorhizic root system usually includes at least two root types: primary roots and lateral roots and are initially dominated by the primary root, which produces lateral roots. Even though adventitious roots are unusual in allorhizic systems, they can occur, particularly in response to wounding they can emerge from the hypocotyl or stems, in particularly in response to wounding (Atkinson *et al.*, 2014, Osmont *et al.,* 2007).

In contrast, the homorhizic root system, which is found in monocotyledones, is characterized by the development of many adventitious roots in parallel to the primary root (Atkinson *et al.*, 2014, Osmont *et al.,* 2007). In contrast to lateral roots, adventitious roots (ARs) are formed from above-ground organs such as hypocotyls, stems and leaves. Unlike lateral roots, which originate from pericycle cells, adventitious roots originate from cambial or other meristematic cells (Leguéa *et al.*, 2014). The majority of the root system in maize and rice the majority of the root system is formed from postembryonic shoot-borne roots. All the root types can branch by forming lateral roots, giving the root system a bushy appearance. Maize forms additional embryogenic roots, which emerge from the scutellar node and are called

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seminal roots. Primary roots of monocotyledons are often also referred to seminal roots (Figure 1) (Dolan *et al., 1993; Osmont et al.,* 2007; Atkinson *et al*., 2014).

Root System Architecture (RSA) - In the context of biology, the word "architecture" usually stands for the spatial configuration of some complex assemblage of subunits, with the implication that the overall configuration has some functional significance (Lynch, 1995). RSA has been described as the spatial configuration of a root system in the soil and the term RSA is generally used to describe the shape and structure of root systems (De Dorlodot *et al.,* 2007).
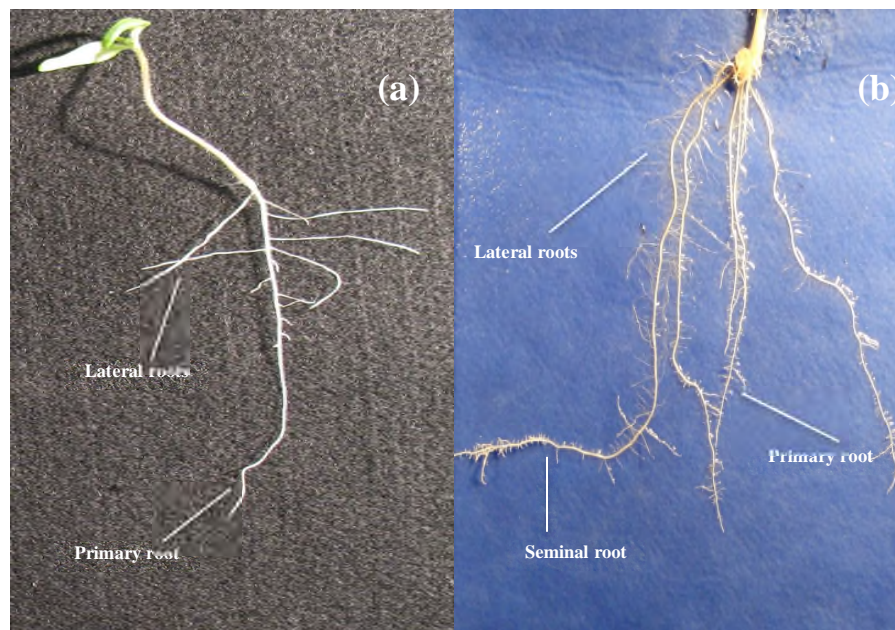

Figure 1. Tomato and rice root system with the major root types indicated. Macroscopic view of 8 day old Tomato (a) and 10 day old rice root system (b).

RSA is known to be highly plastic and strongly affected by environmental conditions (Deak and Malamy, 2005). The primary root is the origin of the plant root system, which is established during embryogenesis. However, the adult plant's root system is made up also of lateral roots and adventitious roots, which form post-embryonically. The number and position of lateral roots is determined by the postembryonic decisions, which affect the size and overall architecture of the root system (Malamy, 2005; Macgregor *et al.,* 2008). RSA affects

plant productivity because the main soil resources are heterogeneously distributed in the soil, so that the spatial deployment of roots will determine the amount of water and nutrients available to the plant, and can be an important factor in the plant's ability to compete for soil resources (Lynch, 1995). Depending on soil composition, differences in RSA may affect the ability to compete for soil resources. RSA can be modulated in several ways: through promotion or inhibition of primary root growth, through growth of lateral roots, through the formation of adventitious roots and through an increase in root hairs (Osmont *et al.*, 2007).

In the past two decades, studies in Arabidopsis have provided detailed insight into root structure. Arabidopsis roots consist of concentric layers of epidermis, cortex, endodermis and pericycle that surround the vascular tissue in the middle of the root. The epidermal cells consist of two types of cells: root hair cells and non root-hair cells. Lateral roots in Arabidopsis originate from pericycle founder cells located opposite xylem poles (Péret *et al.,* 2009). It has been suggested that the pericycle cells that will initiate lateral root primordia continue or stay at least competent to divide after leaving the root apical meristem (RAM) (Dolan *et al.,* 1993; Beeckman *et al.,* 2001). Later on it was shown that the decision to recruit pericycle cells for lateral root formation is taken in the basal meristem, a zone behind the primary root apical mesristem (De Smet *et al.*, 2007). The initiation of lateral roots occurs in the differentiation zone and happens when either one or two pericycle founder cells divide anticlinally to give rise to 8-10 cell layer stage 1 primordia. The cells then divide in a periclinal plane to give rise to another layer. Afterward, daughter cells continue to divide in periclinal or anticlinal planes to create a dome-shaped primordium (spanning stages III–VII) that eventually emerges (at stage VIII) from the parental root (Malamy and Benfey, 1997; Casimiro *et al.,* 2003; Péret *et al.,* 2009).

Though Arabidopsis has been an excellent model for root/lateral root development it is also becoming clear that many plant species show distinctive cellular aspects that are different from Arabidopsis (Ron *et al.,* 2013). For example, Arabidopsis contains only four QC cells whereas most monocot and dicot species contain a greater number of QC cells (Jiang *et al.*, 2003). To date the regulatory mechanisms controlling this diversity in QC cell number are completely unknown. Additionally, most monocot and dicot species unlike Arabidopsis contain numerous cortex layers (Dolan *et al.*, 1993). Even within in the same genus, there could be significant developmental differences. The wild tomato species *Solanum pennellii*

adapted to growing at high altitudes in often near desert conditions in South America contains one less cell layer in the roots compared to the cultivated *Solanum lycopersicum*, *cv.* M82. This extra, complete layer in M82 was found throughout the root and was derived from a cortex- endodermis initial in contrast to a middle cortex layer (Ron *et al.,* 2013).

RSA is controlled by developmental cues and the environment

Genetically identical plants can differ in RSA, depending on their macro- and microenvironment. Factors include nutrient and water availability and distribution status, soil density, salinity and temperature, and interaction with micro-organisms. Even though this plasticity is well documented, the molecular mechanisms underlying it are yet poorly understood (Zhang *et al.,* 1999; Deak and Malamy, 2005; Nacry *et al.,* 2005; Osmont *et al.,* 2007). Nutrients such as nitrate, phosphate, potassium, sulphate and iron can act as signals that roots can be perceived and respond to. Among all nutrients, the quantity of nitrogen (N) and phosphorus (P), have been found to have the greatest effect on RSA (Forde and Lorenzo 2001; Linkohr *et al.,* 2002; López-Bucio *et al.,* 2003). The changes in the internal and external concentration of nutrients can affect important developmental processes, such as root-hair formation, primary root growth and lateral root formation. Abiotic factors that influence RSA can also include light, which can act as a major positive regulator of root branching (Osmont *et al.,* 2007). Here we discuss the role of water and individual nutrients and then bring these abiotic factors together with the role of developmental cues such as plant hormones to control RSA.

Water is the most limiting resource for agriculture, and therefore irrigation has become an important contributor to improved yields. About 83 percent of the water that is consumed (that is, not recycled) is devoted to irrigation (Boyer, 1982). The amount of water required varies greatly between different agricultural types and climatic regions (Morison *et al.,* 2008). In arid and semi-arid environments, water availability varies greatly with soil depth and season and therefore root architecture has a key role in determining the productivity in these environments. Some desert root systems have been identified, with deep taproots, shallow lateral roots (Lynch, 1995). Even though most crop species have been domesticated in less extreme environments, there are wild crop progenitors which are adapted to a wide range of environments including high altitude and desert habitats (Boyer, 1982). The capacity of a root

system for water uptake is important for crop productivity, and this capacity depends primarily on the degree to which the root extends its absorption area. The absorption area, which exhibits genetic variation, is determined by RSA. To date, many studies have reported quantitative trait loci (QTLs) for rice root system characteristics such as mass and depth. However, very little has been clarified about how these QTLs control root system growth at the detailed morphological level (Horii *et al.,* 2006). Therefore, identification and deeper understanding genes regulating these root traits will be crucial for developing strategies for future crop improvement programmes. Cloning and characterization of DRO1 in rice is one such example. DRO1 gene regulates root angle in rice and introduction of DRO1 gene in shallow rooted and drought sensitive but commercially important IR64 variety resulted in deeper roots and improved drought tolerance (Uga *et al*., 2013).

Nitrogen (N) availability is a major factor limiting growth and development of plants (Postma *et al*., 2014; Yu *et al*., 2014; Linkohr *et al.,* 2002; Kraiser *et al.,* 2011). In the biosphere, N is available in different forms, such as inorganic molecular N_2, ammonium or nitrogen oxides, and the organic N (e.g. amino acids). Plants can use all these forms with the proviso that the direct use of molecular N_2 is available only to the plant species living in symbiosis with nitrogen fixing bacteria (Wiren *et al.,* 1997; Zhang *et al.,* 1999). Nitrate has an important impact on LR development, and when the supply of nutrients in soil or media is not uniform, LRs tend to proliferate in a nutrient-rich zone. This has been observed with several different nutrients and many plant species (Ogawa *et al.*, 2014; Robinson, 1994; Casimiro *et al.,* 2003). Genetic and molecular approaches have revealed that nitrogen availability affects lateral root development by three different nitrogen-related regulatory mechanisms: (1) a localized stimulatory effect that acts mainly on the elongation of LR, which is more obvious when plants grown on low nitrate are treated with a localized nitrate supply and is mediated by a putative MADS-box transcription factor, ANR1 (ARABIDOPSIS NITRATE REGULATED 1) (Robinson, 1994; Zhang *et al.,* 1999; López-Bucio *et al.,* 2003); (2) the inhibitory effect, which can be observed when plants are grown on a medium with a uniformly high nitrate concentration immediately after the emergence of the lateral root primordium from the parent root (Zhang *et al.,* 1999; Zhang and Forde, 2000); and (3) inhibition by a high sucrose-to-nitrogen (C:N) ratio, which leads to a dramatic

repression of LR development (Malamy and Ryan, 2001; Casimiro *et al.,* 2003; Malamy, 2005).

Phosphate (P) After N, P is quantitatively the most important nutrient for plant growth (Vance *et al*., 2003; Lambers *et al.*, 2006). It is an essential non-renewable inorganic nutrient for all living organisms; making up about 0.2% of a plant's dry weight as a fundamental component that is present in key organic molecules such as DNA, RNA, ATP, NADPH, and membrane phospholipids, and, therefore, plants cannot grow without a reliable supply of this nutrient (Schachtman *et al.,* 1998). P plays a very important role in most of plant developmental pathways such as energy generation, nucleic acid synthesis, photosynthesis, glycolysis, respiration, membrane synthesis and stability, enzyme activation/inactivation, redox reactions, signaling pathways, carbohydrate metabolism, and nitrogen fixation (Lambers *et al.,* 2006). Though P is prevalent in soil, it is not in its bioavailable form thus making it a major limiting factor for plant growth (Hinsinger, 2001). It can be taken up by plants as inorganic phosphate (Pi) forms $H2PO_4^-$ and HPO_4^{2-}, which occur in soil solutions at very low concentrations (0.1–10 µM) (Vance *et al*., 2003).

To cope with inadequate Pi supply, plants adapt by increasing Pi uptake and recycling through a combination of growth, developmental and metabolic responses (Ogawa *et al*., 2014; Ticconi and Abel, 2004; Tran *et al.,* 2010). One of the key plant responses to low soil Pi includes the secretion of organic acids into the rhizosphere to aid in mobilizing bound organic phosphates which is one of the primary mechanisms facilitating the release of orthophosphate (Tran *et al.,* 2010). Plants in some families (e.g. *Proteaceae*, *Casuarinaceae*, *Fabaceae* and *Myricaceae*) can form dense clusters of lateral roots called 'cluster roots', an adaptation in nutrient-poor soil (Neumann and Martinoia, 2002; Lamont, 2003; Shane and Lambers, 2005). Another adaptation of plants to low phosphorus availability includes symbioses with microbes, notably mycorrhizal fungi (arbuscular mycorrhizae or ectomycorrhizae) (Bolan, 1991; Péret *et al.,* 2011). Developmental responses to inadequate Pi supply can be dramatic changes in RSA such as an arrest of primary root elongation, an increase in lateral root formation and emergence, and an increase in root hair proliferation (Bai *et al.,* 2013; Péret *et al.,* 2011; Bates and Lynch, 1996). When growing with insufficient Pi, RSA changes, resulting in a shallower root system bearing more and longer lateral roots as well as denser root hairs. One of the key transcription factors regulating phosphate

starvation response is PHR1 (phosphate starvation response1). Recently it has been shown that a nuclear protein SPX1 regulates PHR1 activity (Puga *et al.*, 2014). Auxin is also a key regulator of root and lateral root development and plays a key role under P starvation conditions (Deb *et al.*, 2014).

Control of Root Development by Hormones crosstalk

In the nineteenth century, Charles Darwin demonstrated that numerous plant growth processes are regulated by "substances" that move from one part of the plant to another. Almost a century later scientists know that those "substances" are small molecules derived from various essential metabolic pathways which are called plant hormones or plant growth regulators (Santner *et al.,* 2009). Auxin, abscisic acid (ABA), cytokinin, gibberellin and ethylene are the 5 'classical' phytohormones identified during the first half of the twentieth century; all can affect root growth. Moreover, several additional hormones such as brassinosteroids, jasmonate, salicylic acid, nitric oxide and strigolactones have been recognized recently (Santner and Estelle, 2009), and some have been shown to have an impact on the root growth. These plant hormones, which regulate plant growth and development and mediate responses to external environmental stimuli, are small, naturally occurring substances with very diverse chemical natures and structures (Santner and Estelle 2009; Santner *et al.,* 2009; Wolters and Jürgens, 2009; Garay-Arroyo *et al.,* 2012).

Auxin modulates several processes such as the response to light and gravity, control of root and shoot architecture, organ patterning, vascular development and growth in tissue culture (Cho *et al.*, 2014; Woodward and Bartel, 2005; Benková and Hejátko, 2009; Santner and Estelle, 2009; Rodriguez-Villalon and Hardtke, 2014). Auxin plays a crucial role in regulating several key root traits including root angle, root length, root density and is also required for both initiation and emergence of lateral roots (Péret *et al.,* 2009; Fukaki and Tasaka, 2009; Péret *et al.,* 2012; Petricka *et al.,* 2012; Laskowski, 2013; Lavenus *et al.,* 2013). Application of exogenous auxin increases the number of LRs whereas inhibition of auxin transport decreases the number of LRs, indicating a positive role for auxin during LR formation (Casimiro *et al.,* 2001; Nibau *et al.*, 2008; Sun *et al.,* 2009).

Indole-3-acetic acid (IAA), the major form of auxin in higher plants is predominantly synthesized in the shoot apex but it is now known that IAA can also be synthesized in the

roots. It has been shown in Arabidopsis that the emergence of lateral root primordia (LRP) appears to be dependent on shoot-derived auxin in young seedlings (4 to 7 day old) but not in older (7 to 10 day old) seedlings. (Bhalerao *et al*., 2002; Ljung *et al.,* 2005; Swarup *et al.,* 2008). Auxin-induced growth responses in roots have been shown to be the result of downstream changes in expression of several genes including auxin transporters such as LAX3 and cell wall-remodeling enzymes such as pectate lyase, pectin methyl esterase, α-expansin (Swarup *et al*., 2008, Lee *et al.,* 2012), and β-xylosidase genes (Neuteboom *et al.,* 1999; Laskowski *et al.,* 2006). Interestingly, the pectin in the newly forming lateral roots was mainly methylated whilst that in the overlying cells of the parent root was demethylated. This could explain why the LRP is protected from cell wall degradation during emergence (Laskowski *et al.,* 2006; Lavenus *et al.,* 2013). All together these results suggest expression of cell-wall remodeling genes is triggered in the presence of auxin in the overlaying cells that will facilitate primordium emergence through the outer tissues (Swarup *et al*., 2008, Péret *et al.,* 2012). Recently auxin has also been shown to affect lateral root emergence by affecting regulation of aquaporins. These facilitate water movement across cell membranes and auxin appears to repress aquaporin expression in the LRP and overlying tissues thus regulating tissue hydraulics to promote lateral root emergence (Péret *et al.,* 2012). The level of auxin concentration in the root tissue can be modulated by nutrient status. Arabidopsis seedlings transferred from high nitrate (50 mM) to low nitrate concentrations (0.1 mM), show an increase in auxin concentration compared to plants grown continuously in high nitrate. The high level of auxin can be correlated with the release of LRs from high nitrate inhibition when transferred to low nitrate. This may suggest that high nitrate supply might be inhibiting auxin biosynthesis or its translocation from shoot to roots (Vidal and Gutiérrez, 2008). Besides auxin, ABA has also been associated with high nitrate repression of LR growth in an auxin independent pathway (De Smet *et al.,* 2006).

Cytokinins are a class of plant hormones that play positive and negative regulatory roles in many aspects of plant growth and development. They stimulate the formation and activity of shoot meristems, retard leaf senescence, inhibit root growth and branching, and play a role in seed germination and stress responses. They also appear to mediate a number of light regulated processes including chloroplast differentiation (Werner *et al*., 2001; Werner *et al*., 2003). CKs antagonize auxin in many processes including their effect on LR development

where cytokinins suppress lateral root formation. Transgenic Arabidopsis plants with decreased cytokinins levels have been reported to display increased root branching and also enhanced primary root growth (Osmont *et al.,* 2007). Cytokinins receptor mutants *cre1-2* and the *ahk2-5 ahk3-7* double mutant show longer primary roots and increased number of lateral roots (Riefler *et al.,* 2006). Similarly, transgenic Arabidopsis plants overexpressing *AtCKX* (Cytokinin oxidase/dehydrogenase) show an increase in primary root length as well as increased numbers of lateral and adventitious roots (Beemster and Baskin, 2000; Werner *et al.,* 2001; Werner *et al.,* 2003). This behavior has also been shown in rice, where cytokinin has an inhibitory effect on LR initiation and stimulatory effect on LR elongation (Debi *et al.,* 2005). It has been demonstrated that cytokinins regulate early processes involving the lateral root founder cells to disrupt lateral root initiation (Laplaze *et al.,* 2007; Bishopp *et al.,* 2011). The inhibitory lateral root initiation effect of cytokinins can be explained because exogenous Cytokinins block the G2 to M transition in pericycle founder cell activation (Li *et al.,* 2006). The cytokinins biosynthesis and signalling mutants show a higher number of abnormally close LRPs in comparison to wild type plants which can suggest that endogenous cytokinins may be involved in the control of LRP spacing by preventing new LRs to initiate in close proximity to already existing LRPs (Bielach *et al.,* 2012; Lavenus *et al.,* 2013). Like Arabidopsis, the legume *Medicago truncatula* also uses cytokinins signalling to inhibit LR formation. RNA interference of the cytokinins receptor homolog Cytokinin Response1 (*MtCRE1*) led to CK-insensitive roots, which showed an increased number of lateral roots indicating a common role for cytokinins in higher plant LR formation (Gonzalez-Rizzo *et al.,* 2006; Fukaki and Tasaka, 2009). In rice also it has been shown that cytokinins control crown root formation (Gao *et al.,* 2014). Like auxin cytokinins are also known to regulate root system architecture in response to environmental cues (Ramireddy *et al*., 2014).

Both auxin and cytokinins coordinate their activities to regulate various aspects of plant growth and development. In dominant *ren1-D* mutants crown root formation is promoted by rice cytokinin oxidase/dehydrogenase gene *OsCKX4* by mediating the interaction between cytokinin and auxin (Gao *et al*., 2014). In Arabidopsis, cytokinins have been shown to repress protoxylem cell specification but do not block xylem pole pericycle cell fate. Cytokinins did not affect the perception of auxin in lateral root founder cells whereas they block lateral root initiation in lateral root founder cells by inhibiting auxin-induced cell fate

respecification by down regulating PIN gene expression (Laplaze *et al.,* 2007). Merhavy *et al.,* (2014) recently demonstrated a novel cytokinin-driven polarization mechanism that causes a rapid auxin stream redirection in developmental processes such as lateral root organogenesis, in which a gradual PIN polarity switch defines the growth axis of the newly formed organ. They show that auxin efflux transporter PIN1 depletion is enhanced by cytokinin at specific polar domains, thus rearranging the cellular PIN polarities and directly regulating the auxin flow direction (Mehravy *et al.,* 2011; Merhavy *et al.,* 2014).

Gibberellins (GAs) affect a wide range of plant growth, development, and environmental responses, including seed germination, stem elongation, leaf expansion, pollen maturation, induction of flowering and fruit development (Fleet and Sun, 2005; Ueguchi-Tanaka *et al.,* 2007). GAs also foster root development and regulate root growth by controlling cell proliferation and elongation (Fu and Harberd, 2003; Ubeda-Tomás *et al.,* 2008; Ubeda-Tomás *et al.,* 2009; Achard *et al.,* 2009; Garay-Arroyo *et al.,* 2012). The GA-deficient *ga1-3* Arabidopsis mutant has shorter primary roots that can be rescued by GA addition indicating that GA affects primary root growth (Fu and Harberd, 2003). Similarly in Poplar GA-deficient and GA-insensitive mutants show an increase in LR density and elongation, whereas enhanced GAs levels either *in vivo* or *in vitro* inhibited LR development (Gou *et al.,* 2010).

The ability to increase root growth is important for newly germinated seedlings so they can rapidly take up water and nutrients after emerging from their seed coat and also have a better anchorage in the soil (Achard *et al.,* 2009; Ubeda-Tomás *et al.,* 2009; Ubeda-Tomás *et al.,* 2012). The endodermis appears to be the primary responsive tissue for GA regulated root growth (Ubeda-Tomás *et al.,* 2008, Ubeda-Tomás and Bennett, 2010). It has been shown that both GA biosynthesis and the GA response pathway are subject to regulation by auxin (Fu and Harberd, 2003). It has been demonstrated that shoot-derived auxin interacts with GA signals to regulate the levels of DELLA repressors. In addition, activity of enzymes involved in GA biosynthesis is dependent on the polar auxin transport (Fu and Harberd, 2003).

Brassinosteroids (BRs) are a group of plant-oristeroidal hormones with a wide range of biological activity and are essential for normal plant development. BRs are involved in several aspects of plant development, including the stimulation of cell division and

elongation, vascular system differentiation, leaf development, bending, reproductive development, photomorphogenesis and root development. They are also involved in resistance responses against various abiotic and biotic stresses (Clouse and Sasse, 1998; Müssig *et al.,* 2003; Divi and Krishna, 2009; Clouse, 2011). Almost 70 BRs have been identified in plants, with Brassinolide (BL) being the most biologically active (Fujioka and Yokota, 2003; Bajguz, 2007; Wang *et al.,* 2009). Genetic and pharmacological studies have revealed that BRs promote root growth (Li *et al.,* 2002; Müssig *et al.,* 2003; Du *et al.,* 2012). Work in Arabidopsis has revealed that BRs are required for the promotion of cell expansion and cell division in meristematic root cells and that balanced BR signaling is needed for the optimal root growth (González-García *et al.,* 2011; Hacham *et al.,* 2011).

Both BRs and auxin influence plant development and overlapping transcriptional responses to these phytohormones imply an interaction between the two hormonal pathways. It has been shown that in Arabidopsis roots, *BREVIS RADIX* (*BRX*), which is a gene required for optimal root growth is involved in mediating the interaction BRs and auxin interaction. *BRX* belongs to a plant-specific gene family that encodes proteins that are predicted to regulate transcription (Mouchel, 2004; Briggs *et al.,* 2006; Mouchel *et al.,* 2006). The Arabidopsis *brx* mutant has a root-specific deficiency of brassinosteroid. Interestingly, this deficiency affects the root expression level of approximately 15% of all Arabidopsis genes, however the transcriptome profile can be restored to wild type level by brassinosteroid treatment (Mouchel *et al.,* 2006). This work indicates that Auxin strongly induced *BRX* expression while brassinolide mildly repressed BRX expression, suggesting that BRX acts at the centre for maintaining brassinosteroid levels to permit optimal auxin action (Mouchel *et al.,* 2006). Recently it has been proposed that BRs may also regulate root growth in P deficient environment (Singh *et al*., 2014).

Abscisic Acid (ABA) regulates many aspects of plant growth and development including embryo maturation, seed dormancy, germination, seedling growth, lateral root development, cell division and elongation, transition from vegetative to reproductive phase and responses to environmental stresses such as drought, salinity, cold, pathogen attack and UV radiation (Zeevaart and Creelman, 1988; Finkelstein *et al.,* 2002; Chinnusamy *et al.,* 2008). ABA has been shown to affect root elongation in a dose dependent manner, where exogenously applied ABA promotes root elongation at lower concentrations (0.1 mM) but inhibits root growth at

concentrations above 1.0 mM (Ghassemian *et al.,* 2000; Garay-Arroyo *et al.,* 2012). It has been reported that exogenous ABA also inhibits lateral root development in an auxin-independent manner, as the inhibitory effect of ABA could not be rescued by either exogenous auxin application or elevated auxin synthesis (Beaudoin *et al.,* 2000; De Smet *et al.,* 2003). Genetic evidence also supports a role for ABA in regulating root growth. SNF1-RELATED PROTEIN KINASE2.2 (SnRK2.2) and SnRK2.3 are key protein kinases that mediate a major part of ABA signaling in Arabidopsis and the *snrk2.2 snrk2.3* double mutant show strong ABA-insensitive phenotypes in seed germination and root growth inhibition (Fujii *et al.,* 2007).

Interestingly, ABA has a key role in mediating the inhibitory effects of NO_3^- on LR formation. LR numbers are notably reduced in four ABA synthesis mutants (aba1-1, aba2-3, aba2-4 and aba3-2) and two ABA-insensitive mutants (abi4 and abi5) (Signora *et al.,* 2001; De Smet *et al.,* 2006). Other hormones such as auxin have been proposed to act as the long-range signal from shoot to root that mediates high nitrate inhibition of LR growth just after their emergence (Forde, 2002; Walch-Liu *et al.,* 2006).

Ethylene is a plant hormone known to play a central role in several physiological processes, such as leaf and flower senescence, abscission of organs, flower initiation, fruit ripening, and seed germination and it also plays a crucial role during root development and root hair differentiation (Clark *et al.,* 1999; Le *et al.,* 2001; Růzicka *et al.,* 2007; Swarup *et al.,* 2007). Swarup *et al.,* 2007 show that in Arabidopsis ethylene inhibits root growth by regulating the elongation of cells that leave the RAM (root apical meristem) and inhibition of root growth by ethylene is mediated via auxin. This is further supported by studies in tomato where ethylene receptor mutation *Never-ripe* (*Nr*) show increased root mass but fewer adventitious roots (Clark *et al.,* 1999). Treatment with auxin increased adventitious root formation on vegetative stem cuttings of wild-type plants but not in *Nr* plants. Reduced adventitious root formation has also been observed in ethylene-insensitive transgenic petunia plants suggesting that the effect of auxin on adventitious rooting is influenced by ethylene (Clark *et al.,* 1999).

Ethylene has also been demonstrated to affect cell division in the quiescent centre (QC) cells and is likely to be involved in root meristem maintenance (Ortega-Martínez *et al*., 2007). Manipulation of the ethylene pathway genetically or chemically affected the division activity

of the QC. Plants with elevated level of ethylene such as *eto1* mutants show QC cell division independently of auxin and without interfering with QC cell fate (Ortega-Martínez *et al.,* 2007; Thomann *et al.,* 2009).

Strigolactones (SLs) are hormones that regulate many aspects of plant development and in 2008 were identified as being responsible for inhibition of shoot branching (Beveridge, 2014; Bennett and Leyser, 2014); since then rapid progress has been made in understanding their biology. SLs are derived from cleavage of carotenoids and 15 strigolactones have been structurally characterized. They promote root-hair elongation and increase cell numbers in the primary-root meristem while suppressing lateral-root formation under conditions of sufficient phosphate, but they induce it under limiting phosphate (Kapulnik *et al.*, 2014; Koren *et al.*, 2013). They also suppress outgrowth of preformed axillary buds in the shoot, induce secondary growth in the stem, suppress adventitious-root formation and are involved in determining plant height (Beveridge, 2014; Koltai, 2014). In *Medicago truncatula* it has been shown that the application of the synthetic strigolactone analogue GR24 has an inhibitory effect on the lateral root density (De Cuyper *et al.*, 2014). The biosynthetic and signaling pathways of SLs have been reasonably well understood by identification of defective genes from branching mutants of several plant species including Arabidopsis *max* (*more axillary growth*) mutants, pea *rms* (*ramosus*) mutants, petunia *dad* (*decreased apical dominance*) mutants and rice *d* (*dwarf*) mutants (Germain *et al.*, 2013; *Zheng et al., 2014*).

Conclusion

Crop production must double by 2050 to keep pace with global population growth (Lavenus *et al.,* 2014). One way to reduce the negative impact of climate change on yield is to manipulate RSA in favour of improved distribution of roots in the soil to enhance water and nutrient uptake. Advances in root phenotyping and imaging using non invasive approaches such as X-ray computed tomography (Bao *et al.*, 2014) and magnetic resonance imaging (Metzner *et al.*, 2014) are very promising and are likely to provide better understanding of RSA. Using X-ray computed tomography recently Bao *et al.*, (2014) revealed a novel hydropatterning mechanism highlighting the importance of these non invasive approaches to study RSA. Deeper understanding of RSA in soil and how RSA responds to environment signals such as changes in nutrient and water availability in soil and interaction with soil

microflora will be crucial. These signals act through distinct signal transduction pathways involving a plethora of intrinsic factors including not only hormones as discussed above but also other signals such as microRNAs (Sorin *et al*., 2014), NO (Correa-Aragunde *et al*., 2004) and ROS (Manzano *et al*., 2014). However, molecular connections between these pathways are less understood, and it remains an outstanding question how different signaling pathways coordinately regulate RSA. Deeper understanding of the molecular mechanisms controlling key root traits will be crucial for developing strategies for future crop improvement programmes. Accurate phenotyping, modelling and input from farmers and breeders will help define ideal RSA for different crops and target environments and will result in the development of crops with improved water and nutrient uptake efficiency to improve yield and will be a big step forward towards meeting challenges of increasing future food demand in an environmentally friendly and sustainable manner.

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