Plant Growth Regulation (2018) 85:337–349
https://doi.org/10.1007/s10725-018-0397-1

REVIEW PAPER

Simplifying the root dynamics: from complex hormone–environment interactions to specific root architectural modulation

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Received: 3 July 2017 / Accepted: 6 April 2018 / Published online: 8 May 2018

Abstract

The recent unveiling of the intriguing interactions among phytohormones and environmental cues in regulating root architecture for optimum plant acclimation has opened new avenues for research. Additional functions of transcriptional as well as protein-level regulators are being identified, uncovering novel interactions between hormonal and environmental signaling pathways, for shaping the root system architecture (RSA). Owing to the importance of root architectural dynamics under constantly encountered external factors, it is crucial to have a regular and comprehensive update of these interactions, affecting RSA, in order to improve crop performance. Moreover, it is equally important to identify and highlight, in crop species, the crucial regulators, which actively mediate hormonal as well as hormone–environment interactions, but have so far been characterized only in model plants such as Arabidopsis. Such updates will open up new research possibilities for plant biologists in extending the present knowledge on root system plasticity from Arabidopsis to economically important crop plants. Here, we provide a consolidated review of the recent findings on novel inter-hormonal and hormone–environment interactions with special emphasis on key downstream regulators and signaling pathways. We conclude by dissecting the gaps and challenges encountered at present, with an outline for future perspectives to channel the enormous information on hormone–environment regulation of RSA, towards a common output in the form of specific modulation of RSA components.

Keywords Hormone–environment interactions · Regulatory factors · Roots system architecture · Signaling networks

Introduction

The term “root plasticity” holds a special meaning for plant biologist’s today, given the large number of recent breakthroughs in the study of root architectural dynamics (Villordon et al. 2014; Lupini et al. 2014). Our understanding has long surpassed a simple view of roots as anchorage and nutrient-uptake system, as evident, for example, in recent discoveries about the signaling mechanisms and regulatory factors by which plants modify their root architecture to acclimate to changing environments (Javaux et al. 2008). Attention continues to be focused on unraveling transcription factors, microRNAs and enzymes that bridge the pathways between hormonal and environmental signals, to orchestrate root developmental plasticity (Nizampatnam et al. 2015; Wang et al. 2017).

Roots system architecture (RSA) refers to the three dimensional branching pattern of lateral roots and root hairs around the primary root and the major components of RSA include the root apical meristem, root hairs, root angles and lateral roots (Orman-Ligeza et al. 2014). RSA patterning is a highly regulated trait, influenced by the action of inter-hormonal as well as hormone–environment factors that, need to be integrated systematically in the plant via specific downstream regulators (Monzón et al. 2012). This integration of factors can be described as an interaction that results in the shaping of specific RSA components. For example, Bao et al. (2014), demonstrated that lateral root formation is regulated by root moisture availability, a phenomenon known as “hydropatterning” which acts upstream of auxin signaling in determining the position of the lateral root founder cell (FC) through the local regulation of TAA1 (tryptophan aminotransferase of Arabidopsis 1) and PINOID-FORMED 3 (PIN3) proteins. This shows that water availability interacts with auxin signaling pathway for shaping the RSA. In

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another spotlight article, Lavenus et al. (2016), revealed complex new aspects of inter-hormonal interaction, wherein auxin and cytokinin antagonize to cause transcriptional regulation of PIN proteins leading to RSA modulation.

Further, it has been recognized that quantitative trait loci (QTLs) associated with RSA have high potential as breeding targets for crop improvement under adverse environmental conditions (Paez-Garcia et al. 2015). To realize this potential, the need of the hour is to gain insight into RSA plasticity through an integrated analysis of the huge mesh of interconnected inter-hormonal as well as hormone–environment signaling networks that influence RSA. Much of the extensive new research on RSA regulation by hormones, environmental factors and hormone–environment crosstalks (i.e., the overlapping of the downstream signalling pathways) is summarized in a number of recent reviews (Liu et al. 2014). However, due to the complexity and vastness of the area, most of the reviews related to root architecture only focus on hormonal aspects or hormone–environment interactions to a limited extent. Thus, it is essential to present a comprehensive report on recent updates in hormone and environment-mediated root architectural plasticity, particularly with respect to individual RSA components. In the present review, we provide such a comprehensive update on RSA modulation under four broad headings including, (1) inter-hormonal interactions regulating specific RSA components under non-stress conditions, (2) crucial hormone–environment interactions affecting the RSA, (3) mechanism of integration of various hormone–environmental signaling pathways with key downstream regulators and (4) gap and challenges, at present, for understanding RSA modulation with an outline for possible future prospects.

Effect of inter-hormonal interactions on RSA components

Root meristem maintenance

Inter-hormonal interactions are evidenced right from embryogenesis for mediating cell fate specification. At the 32 cell-stage embryo stage, localization of the auxin efflux protein (PIN7) reverses from basal (suspensor) to the apical cell and as a result, auxin gets accumulated in the uppermost cell of the suspensor, which becomes the founder cell for the root meristem of the embryonic root, i.e., hypophysis (Su et al. 2011). Later, following cell divisions in the hypophysis, cytokinin signaling is carried out in the apical daughter cell which is destined to become the quiescent center (QC), while cytokinin signaling is repressed in the basal daughter cell of hypophysis via auxin-mediated activation of cytokinin signaling repressors, ARR7 and ARR15 (Su et al. 2011). The root meristem structure consist of three specific zones, i.e., the proximal meristem zone including the QC, transition zone (TZ) and the elongation–differentiation zone (EDZ) and root growth rate is strongly determined by the size (including cell number and volume) of the root meristem, which in turn is dependent on the balance between cell division, expansion and differentiation. It was observed that cytokinin antagonizes auxin at the TZ and determines root meristem size by controlling the differentiation of meristematic cells. At the molecular level, the cytokinin response transcription factor (ARR1) binds the promoter of the protein SHORT HYPOCOTYL 2 (SHY2) (a member of Aux/IAA gene family) and activates it, which in turn represses the PIN genes, while auxin counteracts cytokinin effect by degrading the SHY2 protein (Dello Ioio et al. 2008). Thus, interaction between auxin and cytokinin signaling pathways contribute towards maintenance of the root meristem structure. A recent study on Arabidopsis root demonstrated that the *Pleotropic Regulatory Locus 1* (PRL1) gene coding a WD40-repeat protein subunit ensures the QC confined expression of the transcription factor WUSCHEL RELATED HOMEOBOX5 (WOX5) and is required for maintaining optimum levels of PLT1/PLT2 (PLETHORA family of AP2 transcription factors), which in turn modulates the auxin-dependent maintenance of the root meristem (Ji et al. 2015). Thus, SHY2, PRL1, WOX5 and PLTs acts as important downstream regulatory factors in the auxin–cytokinin mediated maintenance of root meristem, but further experimental inputs are required to decipher the complete regulatory pathway.

Another complicated interaction involving auxin, cytokinin and gibberellin is found in the regulation of root meristem cell transition from division to elongation and differentiation. It is known that PIN gene expression is restricted by the auxin repressor AUX/IAA gene *SHY2*, which is under control of the Arabidopsis response regulator (ARR) transcription factors (ARR1, ARR2) and these ARRs are the final expression targets of cytokinin signaling pathway (Su et al. 2011). Several days after germination, down-regulation of polar auxin transport due to repression of PIN genes in the root meristem cells, triggers initiation of cell elongation and differentiation and restricts cell division. However, during early stages of germination, PIN gene suppression is overcome by the activity of high levels of gibberellins, which inhibits the ARR1 expression through destabilization of DELLA factor RGA (repressor of *ga*1) (Depuydt and Hardtke 2011) and hence, active cell division within root meristem cells is favored during germination. Further with the help of fluorescent labeling method, it was shown that gibberellins are synthesized in root meristematic, cortical or epidermal cell layer and gets transported towards the endodermal cells of the root EZ, suggesting a crucial role of gibberellins in regulating the process of cell elongation in the EZ of root meristem (Shani et al. 2013). On the other hand, auxin also enhances the expression of the ethylene biosynthetic enzyme 1-aminocyclopropane 1-carboxylic acid (ACC) synthase in the root meristems, while ethylene is found to negatively regulate proliferation of cells in the Arabidopsis root meristem and causes endoreduplication (Street et al. 2015). At the molecular level, auxin–ethylene interaction mediates the ethylene-dependent inhibition of cell division at root apical meristem via the SHY2 transcription factor. Thus, SHY2 acts as a common point for cytokinin and ethylene interaction with respect to regulation of root meristem size.

The jasmonic acid (JA) pathway also interacts with the auxin pathway to maintain root meristem. The JA repressor JASMONATE ZIM DOMAIN (JAZ) inhibits the MYC2 transcription factor, which was reported to repress the PLTs (PLT1 and PLT2), while auxin gradient is known to determine the expression of PLTs for root meristem maintenance (Chen et al. 2011; Kazan and Manners 2012). From the above discussions, it is clear that interaction between auxin–cytokinin, cytokinin–gibberellin, auxin–ethylene and auxin–jasmonic acid contributes in initiating and maintaining the root meristem structure.

Root hair formation

Highly specialized outgrowths of root epidermal cells (trichoblasts) playing a crucial role in water and mineral absorption are known as root hairs. Development of root hairs involves three events: cell-fate specification, initiation and elongation, wherein a specific epidermal cell is destined to develop into a root-hair, followed by formation of root hair primordium, which finally elongates to become a mature root hair (Datta et al. 2011). Auxin plays a crucial role in selection of initiation site for root hair and the gaseous hormone, ethylene acts synergistically with auxin to facilitate root hair formation (Muday et al. 2012). Throughout plant life, the shape and size of the root hairs get modulated in response to developmental and environmental cues, which are primarily integrated via auxin signaling pathway, but recently, other hormones were also shown to take significant part in mediating such integration (Zhang et al. 2016). Based on the expression levels of the auxin influx carrier AUX1, it has been postulated that auxin is accumulated in non-hair cells and the continuous supply of auxin from non-hair to hair cells is essential for root hairs to attain optimum elongation (Jones et al. 2009).

The interaction between brassinosteroid and ethylene in regulating root-hair growth and development is also well characterized. In general brassinosteroid promotes, while ethylene inhibits cell elongation in roots. It has been demonstrated that differential expression of the brassinosteroid receptor BRASSINISTEROID INSENSITIVE 1 (BRI1) between the hair and non-hair containing cells is crucial for modulating the growth pattern of these cells (Fridman et al. 2014). It is shown that reduced BRI1 activity in hair cells results in increased brassinosteroid signaling in the neighboring non-hair cells, which in turn triggers expression of the ethylene biosynthetic genes, ACS (1-amino cyclopropane 1-carboxylate (ACC)-synthase) genes mediated partially via the BES1/BZR2 (BRASSINAZOLE-RESISTANT1 (BZR1) and BRI1-EMS SUPPRESSOR1) transcription factor based signaling pathway (Fridman et al. 2014). The enhanced accumulation of ethylene inhibits unidirectional cell expansion in the non-hair epidermal cells and also stimulates local deposition of crystalline cellulose.

Lateral root development

Lateral root patterning is the most conspicuous component of the RSA, which is regulated by a number of inter-hormonal interactions. Ethylene inhibits lateral root formation by enhancing the expression of auxin efflux carriers PIN3 and PIN7, resulting in depletion of auxin maxima from the sites of lateral root initiation (Lewis et al. 2011). It is now shown that such stimulation of auxin efflux by ethylene is dependent on a short 36 amino acid long peptide, POLARIS (PLS) which is strongly expressed in the Arabidopsis roots (Liu et al. 2013). The PLS peptide is a key downstream regulator, which mediates inter-hormonal interactions, for regulating root development (Liu et al. 2014). However, identification and functional characterization of PLS peptide with respect to RSA modulation in economically important plants is still far from complete.

Recently discovered phytohormone, strigolactone regulates PIN protein localization and found to antagonize auxin in regulating lateral root development. This interaction is mediated via reduced glutathione (GSH) and a strigolactone signaling component MORE AXILLARY GROWTH2 (MAX2), which is a subunit of the SCF E3 ligase (Marquez-Garcia et al. 2014). It was demonstrated by using GR24 (a strigolactone analog) treatments, that strigolactones inhibit lateral root development by specifically affecting the lateral root priming (at the root meristem zone) and emergence process near the root–shoot junction (Jiang et al. 2016). The underlying mechanism involves an interaction between strigolactone, auxin and cytokinin, wherein GR24 treatment causes a decline in PIN1 expression through cytokinin signaling components such as ARABIDOPSIS HISTIDINE KINASE 3 (AHK3), ARR1/ARR12 and SHY2, which promotes this strigolactone-mediated inhibition of PIN1. As a result, the auxin flux and lateral root development is inhibited (Jiang et al. 2016).

The popularly known stress hormone abscisic acid (ABA), also inhibits lateral root development under normal physiological conditions (Guo et al. 2009). Studies have shown that *fca-1* mutant, which was initially considered as an ABA receptor (Razem et al. 2006) showed considerable differences from the usual ABA-responses during lateral root development, i.e., in the wild type, ABA significantly inhibited lateral root development while in the *fca1* mutant there was only a marginal decline (De Smet et al. 2003). Though, there were some controversies in considering whether FCA binds ABA or not (Risk et al. 2008), it has been proved undoubtedly that ABA, definitely plays significant role during different stages of lateral root development. However, the key downstream signaling mediators for ABA interaction with other phytohormones for RSA modulation are yet to be identified.

Root angle regulation and growth

It is very well established that modulation of root angle and growth is primarily controlled through gravitational forces, wherein the root bends in response to gravitational stimulus, mediated through positional maxima of auxin followed by auxin-mediated degradation of the Aux/IAA repressor proteins (Cholodny and Went hypothesis, Hayashi 2012). Gravitational signals, are perceived at the root cap region, wherein the sedimentation pressure of the starch containing amyloplasts (statoliths) within specialized cells called as statocytes (gravity sensing cells) were the actual signals for RSA modulation (Morita 2010). Recently, Uga et al. (2013) have demonstrated that alteration of RSA improves drought avoidance through the cloning and characterization of DEEPER ROOTING 1 (DRO1), a rice QTL controlling root growth angle which is negatively regulated by auxin and is linked to gravity-induced downward bending of the root tip. Crucial breakthroughs in the area of root growth response have been achieved. Here, by utilizing a novel Aux/IAA based reporter, i.e., domain II (DII)-VENUS consisting of a constitutively expressed fusion of the auxin-binding domain (DII) of the Aux/IAA28 protein to a variant of yellow fluorescence protein (YFP), VENUS and a mathematical model based on ordinary differential equation (ODE), researchers have quantified the kinetics of auxin redistribution upon gravity stimulus by observing the DII-VENUS degradation rate (Band et al. 2012). This novel approach successfully demonstrated that within minutes after perception of a 90° gravity stimulus, auxin is quickly redistributed to the lower side of the root. But upon reaching the bending midpoint, i.e., ~40° to the horizontal the auxin asymmetry is lost, indicating that after this point the root bending is dependent on other downstream auxin activated effectors. Thus, regulation of root angle is the outcome of interaction between gravitational signals and auxin. Further, the pattern of root bending and induction of FC at the root tip was found to be regulated periodically via an oscillatory gene expression mechanism, wherein DR5 promoter regulated genes at the root meristem region showed periodic expression every 6 h interval (Miguel et al. 2010). Overviews of all the major hormonal interactions, influencing specific components of RSA along with their potential downstream regulators have been illustrated in Fig. 1.

Hormone–environment interaction for RSA modulation

The root architectural plasticity is required at almost each step of root development, as plant's constantly encounters one or the other environmental restrains, majorly in terms of water and nutrient availability in the soil along with other biotic as well as abiotic factors. Majority of the environmental factors modulating RSA acts in close proximity with roots. However, recent studies have indicated that atmospheric factors such as elevated CO_2 which is primarily perceived by the shoot system can also indirectly affect the root architecture. Elevated CO_2 enhances photosynthetic efficiency (till feedback inhibition by excess sugar accumulation takes place), which in turn leads to increased carbon allocation to active sinks such as roots, leading to enhanced lateral root growth and branching (Sreeharsha et al. 2015). Here, we try to consolidate the RSA modulation by environment–hormone interaction focusing majorly on some of the crucial environmental factors affecting root architecture, i.e., drought, salinity, nutrient availability and elevated CO_2 conditions.

Drought–hormone interaction

Water availability to root systems has always been the most crucial factor regulating RSA. Both integration of hormonal signals for shaping the root architecture and perception of environmental cues such as drought for RSA plasticity is mediated through the root apical meristem (RAM). Drought brings about a premature differentiation of RAM by interacting with ABA signaling pathway and results in decrease in RAM size and primary root growth. This modulation of RSA component via drought–ABA interaction helps in tolerating the osmotic stress and was implied as one of the important mechanism of RSA plasticity under drought stress (Ji et al. 2014). Progressive water deficit have been shown to cause inhibition in primary root growth rate as well as decrease in lateral root density in mung bean (Sengupta et al. 2011). In Arabidopsis, R2–R3 type myeloblastosis transcription factor, MYB 96 regulates the activation of lateral root meristem under drought through ABA–auxin interaction, wherein enhanced MYB96 causes up-regulation of Gretchen Hagen 3 (*GH3*) genes encoding auxin-conjugating enzymes and leads to reduced growth and lateral root formation and enhanced drought tolerance ability. While MYB96 deficient mutants

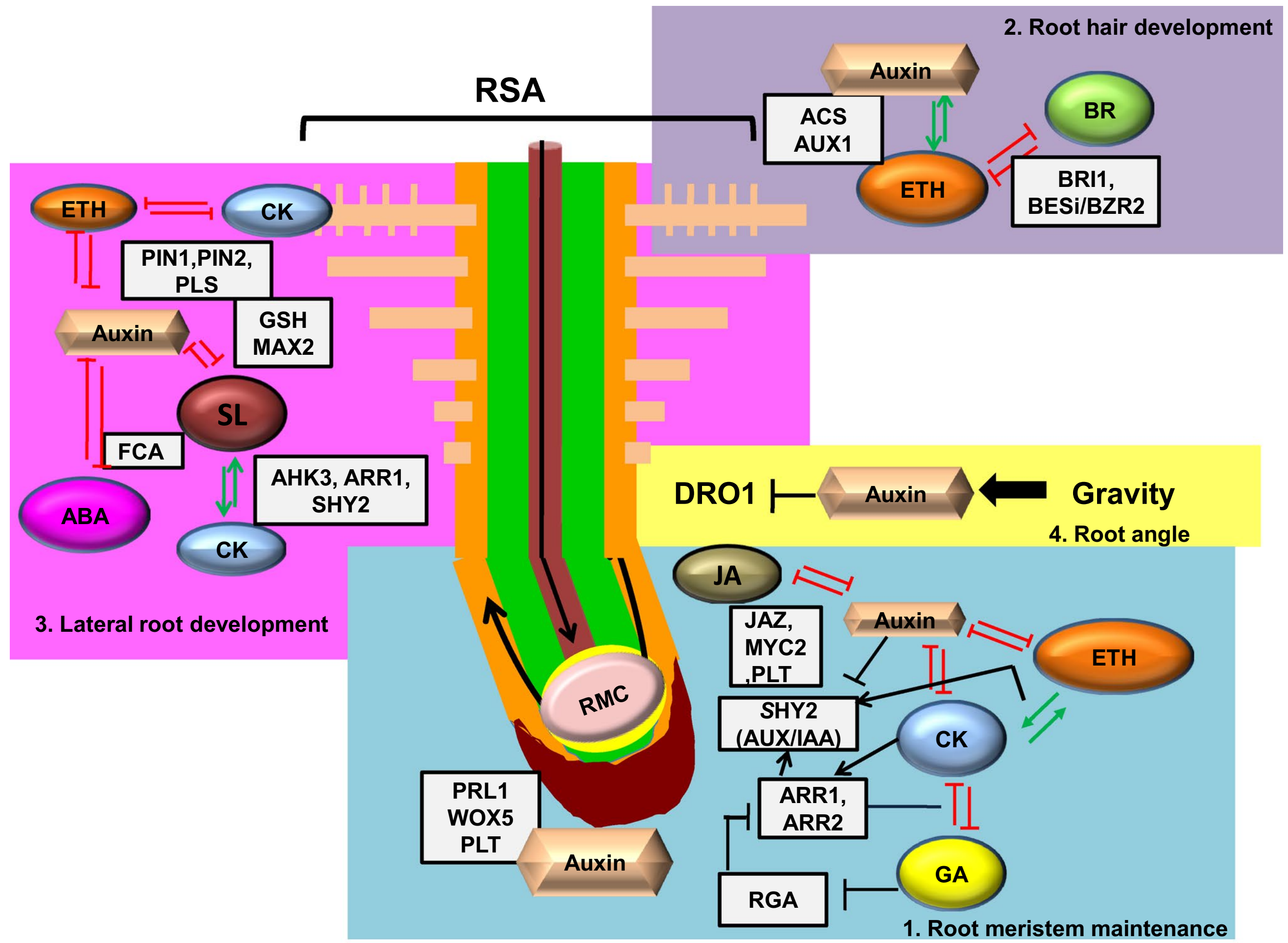

Fig. 1 Generalized overview representing the various inter-hormonal cross-talks along with their respective downstream regulatory components contributing to specific RSA modulation. Red lines with inhibitory symbols indicate antagonistic cross-talk while the green arrows depicts synergistic interaction between two hormones. *ACCS* amino-cyclopropane carboxylic acid synthase, *ARFs* auxin response factors, *ARE* auxin response elements, *HKR* histidine kinase receptor, *CK* cytokinin, *ETH* ethylene, *LR* lateral root, *RH* root hair. (Color figure online)

are susceptible to water deficit and have more lateral roots (Seo and Park 2009).

Now, with the recent demonstration of the moisture control of lateral root initiation, it has become clear that soil crevices containing air instead of water (as is the case in gradually drying soils during progressive water deficit treatments), inhibits lateral root development in those areas and only small root hairs arise (Bao et al. 2014). It was observed that "hydropatterning" occurs during the founder cell (FC) specification stage of lateral root development and the auxin signaling pathway acts downstream to water availability signals for executing the actual "hydropatterning". Though ABA is known to be a "stress hormone" due to its rapid induction under stress conditions specially drought and salinity (Raghavendra et al. 2010), "hydropatterning" of lateral root development is not dependent on ABA but in turn depends on the accumulation of auxin in the cells directly in contact with water. This water induced accumulation of auxin is mediated via the up-regulation of TRYPTOPHAN AMINOTRANSFERASE of ARABIDOPSIS 1 (*TAA1*) gene in the outer tissue layer, which is required for producing the direct precursor of auxin biosynthesis from tryptophan, i.e., indole pyruvic acid (Bao et al. 2014). As a whole, the moisture signals were perceived and transduced via the auxin signaling pathway from the outer tissue layers towards the pericycle and contributes in determining the FC of lateral roots. Newly emerging carotenoid derivatives acting as phytohormones, such as strigolctones are known to mediate both endogenous and exogenous signaling in response to various environmental cues (Pandey et al. 2016). It has been shown recently that strigolactones could act as root-derived systemic signals for drought stress avoidance (Visentin et al. 2016). Under drought stress, strigolactone concentrations usually decline in the roots and it was demonstrated, using grafting of wild type scions of tomato onto strigolactone-deficient root stocks that low levels of strigolactones in the roots act as signals for up-regulating local strigolactone biosynthetic genes in the leaves and thus, primes the shoot system for drought avoidance by becoming hypersensitive to ABA.

Further, through transgenic approach in rice, it was demonstrated that a close interactive network exists between cytokinin, jasmonic acid and brassinosteroid signalling under drought stress, wherein cytokinin overexpressing [transformed with isopentenyl transferase (*IPT*) gene under senescence associated receptor protein kinase (SARK) promoter] transgenic plants were found to overcome the deleterious effects of drought by a simultaneous activation of BR and down-regulation of JA signaling pathway components (Peleg et al. 2011). As a whole, the drought–hormonal 'interaction' primarily brings about a cessation in root growth and lateral root emergence but enhances the overall length of the lateral roots for combating the drought-induced osmotic stress.

Salinity–hormone interaction

The root meristem size gets reduced under salt stress leading to inhibition in root elongation. Recently, the mechanism underlying the salt-induced reduction in root meristem size was reported, which described that salinity stress interacts with auxin signaling via nitric oxide (NO). Briefly, salt stress signals were perceived and results in increase in NO levels in the roots, followed by repression of the PIN gene expressions and stabilization of the AUXIN RESISTANT 3 (AXR3), which is the repressor of auxin inducible genes. As a result, auxin levels are decreased and auxin signaling gets inhibited leading to a reduced root meristem size (Liu et al. 2015). Apart from auxin, jasmonic acid is also found to interact with salt stress signaling for RSA modulation. Specifically, auxin–jasmonic acid interaction inhibits primary root growth, and is mediated via the destabilization of JAZ3 protein, which is a negative regulator (repressor) of jasmonic acid responsive genes (Valenzuela et al. 2016). It was shown previously that jasmonic acid-insensitive mutants have a stabilized JAZ3 protein and phenotypically showed higher primary root growth rate under short term salt stress treatments when compared to the wild types (Geng et al. 2013).

Enhanced salt concentrations were found to inhibit initiation and organogenesis of lateral roots, but significantly promote elongation of the existing lateral root primordia (Wang et al. 2009). However, moderate salinity conditions stimulated primary root growth but the same was significantly arrested under high salt stress. The mechanism underlying the salt-induced modulation involves an interaction between salt stress signals and auxin, wherein high salt signals lead to redistribution of auxin in a direction outwards from the apex and inwards to the epidermis of EZ, resulting in reduced cell division and elongation at the apex causing primary root growth arrest. However, mild salt stress signals (~ 25 mM NaCl for *A. thaliana*) induced slight accumulation of auxin at the root tip which stimulated the primary root growth (Zolla et al. 2010). Salt-induced plasticity in lateral root proliferation and primary root growth involves the calcium binding protein (salt overly sensitive 3; SOS3), wherein SOS3 deficient mutants were found to show 50% reduction in the lateral root primordia activation and a complete inhibition of lateral root emergence. Further SOS3 was found to be essential for auxin biosynthesis and maintenance of auxin gradient under salt stress (Zhao et al. 2011). Hence, salt–auxin interaction for RSA modulation is mediated via SOS3. Components of SOS signaling pathway were also implicated in development and maintenance of root hairs under salt stress (Wang et al. 2008). Broadly, salinity–hormonal interactions majorly bring about inhibition in primary root growth, lateral root initiation and emergence but promote proliferation of existing lateral roots. However, more information needs to be integrated through experimental findings regarding the actual molecular mechanisms orchestrating modulation of individual RSA components via salt–hormonal interactions.

Sugar–hormone interaction

Sugars, apart from being the major energy providing metabolite, also act as key signaling molecules for regulating the overall plant growth and development. Hence, interaction between sugar and various hormonal pathways becomes inevitable with respect to root architectural dynamics. A close interaction among glucose and auxin response pathway for controlling the root growth has been already evidenced (Mishra et al. 2009). When analyzing sugar–hormone crosstalk, the primary regulator is the sugar dependent kinase, TARGET OF RAPAMYCIN (TOR), which is also synonymed as the central hub in primary and secondary metabolism. Specifically, TOR kinase was reported to control the root meristem activation and also regulates the root development related processes by integrating the sugar (nutrient) status of the plant. Further, TOR was also assumed to play a role in regulating root hair growth (Xiong and Sheen 2014). The mechanism of glucose-TOR signaling pathway for root meristem activation, initiates from the photosynthetically-derived glucose in the shoot system, which activates the TOR signaling cascade through glycolysis and mitochondrial bioenergetics and finally activates the root meristem. Further, the transcription factor E2Fa was revealed as the substrate for TOR kinase indicating the existence of an alternate glucose dependent regulation of cell cycle in the root meristem (Xiong et al. 2013).

Interestingly, activation of shoot meristem via TOR signaling pathway requires the presence of another factor, i.e., light apart from glucose signals for activation. Recently, it was proved that in absence of light, exogenous auxin treatment can efficiently complement the light effects and activates TOR signaling pathway in shoot system. Hence, it was proposed that auxin and glucose signaling can interact to regulate the TOR mediated activation of root meristem, as though roots are devoid of light, a local auxin maxima occurs at the root tip region (Li et al. 2017). Thus, sugar–hormone crosstalks also plays an important role in modulating RSA components and might act as potential alternative signaling pathways for root architectural modulation under stress conditions.

Nutrient–hormone crosstalks

When coming to RSA dynamics in response to nutrient availability in general, it was observed that plant's nutritional status during various developmental stages act as systemic signals, while local availability of nutrients acts as stimulatory signals for various RSA components (Caffaro et al. 2011; Giehl et al. 2014). Deficiency of three crucial nutrient, i.e., N, P and Fe is rapidly sensed by plants and results in a dynamic RSA modulation, specifically via auxin signaling Further, there was nutrient-specificity for modulation of specific RSA component, which paves way for further research into the specific receptors and signaling components mediating such regulation in RSA traits. Under high levels of soil nitrate, there is an overall inhibition of lateral root outgrowth, development and elongation. However, within the high N area, soil patches containing high inorganic nitrogen shows a local, stimulatory effect on lateral root elongation and branching (Guan et al. 2014; Guo et al. 2017). In general, nitrate deficiency is found to interact with the auxin signaling pathway for modulating various RSA components. For example, miR393 regulated auxin receptor, auxin signaling F box protein 3 (AFB3) along with their downstream target NAM/ATAF/CUC 4 (NAC4), cause changes in the RSA in response to nitrate deficiency (Vidal et al. 2013). Also, lateral root initiation, development as well as nodulation in soybean roots were found to be stimulated by the AUXIN RESPOSNE FACTOR 8 (ARF), during N deficiency (Wang et al. 2015). It was further demonstrated that the tryptophan aminotransferase related 2 (TAR2) gene, which is involved in the auxin biosynthetic pathway, gets significantly induced in the roots and plays a crucial role in mediating the lateral root growth dynamics under low N conditions (Shao et al. 2017).

A recent study by Araya et al. (2014) identified that the N-responsive signaling peptide CLE (CLAVATA3/ESR-related) and CLV1 (CLAVATA 1) leucine rich receptor like kinase plays a crucial role in modulating lateral root outgrowth under N-deficient conditions by restricting the emergence of lateral root primordia. In Arabidopsis, the ANR1 gene coding for a MADS Box protein was reported to play the role of positive regulator for NO_3^- mediated RSA modulation which in turn gets modulated by the dual affinity nitrate transporter NRT1.1 which is induced by auxin and causes lateral root repression in low nitrate regions (Zhang and Forde 1998; Guo et al. 2002). Recently, using a yeast one hybrid system and a nitrate enhancer DNA, Guan et al. (2014) have identified a transcription factor TEOSINTE BRANCHED1/CYCLOIDEA/PROLIFERATING CELL FACTOR-20 (TCP-20), which was found to play a crucial role in development of preferential lateral roots in NO_3^- rich areas (better known as nitrate foraging) by binding to a number of nitrate regulated genes. Phosphate (P) deficiency is known to cause repression of primary root growth. The underlying mechanism of P deficiency mediated alteration in RSA was recently unveiled, wherein it was shown that the jasmonic acid biosynthetic gene OPR3 (oxophytodienoic acid reductase) suppresses root tip growth during P deficiency and thus inhibits primary root growth, independent of jasmonic acid signaling pathway (Zheng et al. 2016). However, OPR3 was found to interact with ethylene and gibberellin pathways, as well as affect polar auxin transport under P limitations. Under P and N deficiency, strigolactone levels are found to increase in roots and root exudates (Sun et al. 2014).

Iron (Fe) being a crucial component of an array of metabolic enzymes, rapid adaptive responses gets triggered under Fe deficiency in plants, in order to mobilize less soluble Fe compound and enhance Fe uptake. Well established adaptive mechanisms during Fe deficiency include the induction of Fe(III) chelate reductase and activation of proton extrusion in the roots. Recently, it was proved based on reciprocal grafting experiments that Fe limitation-induced adaptive responses are auxin dependent (Wu et al. 2012). Further, it was also deciphered using different NO related Arabidopsis mutants, that NO acts downstream to auxin to induce the Fe(III) chelate reductase during Fe deficiency via the *FIT* (basic helix–loop–helix transcription factor)-mediated transcriptional regulation (Chen et al. 2010). As an overview, specific nutrient availability/deficiency directly or indirectly interacts with major hormones such as auxin, cytokinin and strigolactones and results in specific alteration of RSA.

Elevated CO_2–hormone interaction

Due to the high significance of the impact of global climate change upon plant growth responses, it is necessary to have an integrated analysis on how elevated CO_2 concentration affects the RSA of plants. Unfortunately, the growth responses of plants under high CO_2 conditions varies significantly based on plant's genotypic constitution as well as other co-existing soil and environmental factors (Reddy et al. 2010; Bunce 2014). Thus, a generalized concept of elevated CO_2-mediated RSA modulation cannot be determined. However, when the collective response of CO_2 responsive plants are analyzed, it is observed that elevated CO_2 enriches the photoassimilation rates and in turn, enhances the primary root growth rate as well as the overall lateral root branching patterns. Elevated CO_2 is shown to enhance the cytokinin levels in leaves under low N conditions (Yong et al. 2000). In *Arabidopsis thaliana*, grown under low N and high CO_2 resulted in high C/N ratios due to faster depletion of N and led to enhanced lateral root formation through increased auxin and decreased cytokinin levels (Hachiya et al. 2014). Using reciprocal grafting of shoots and roots between wild-type and receptor mutants is shown that shoot-derived cytokinin can act as shoot–root signal for modulating nodule developmental patterns (Sasaki et al. 2014). Now, analyzing the impact of high CO_2 in modulating RSA levels and also identification of other key components taking part in transducing the atmospheric CO_2 signals into root architectural modulations opens up a very interesting future research perspective. In order to identify the shoot derived signals activated by the elevated CO_2 stimulus, which affects the root architecture, a reciprocal grafting approach using hormonal mutants would be highly useful. A consolidated illustration depicting the 'interaction' between specific hormonal pathways with drought, salinity, nutrient deficiency and elevated CO_2 conditions in modulating RSA was given in Fig. 2.

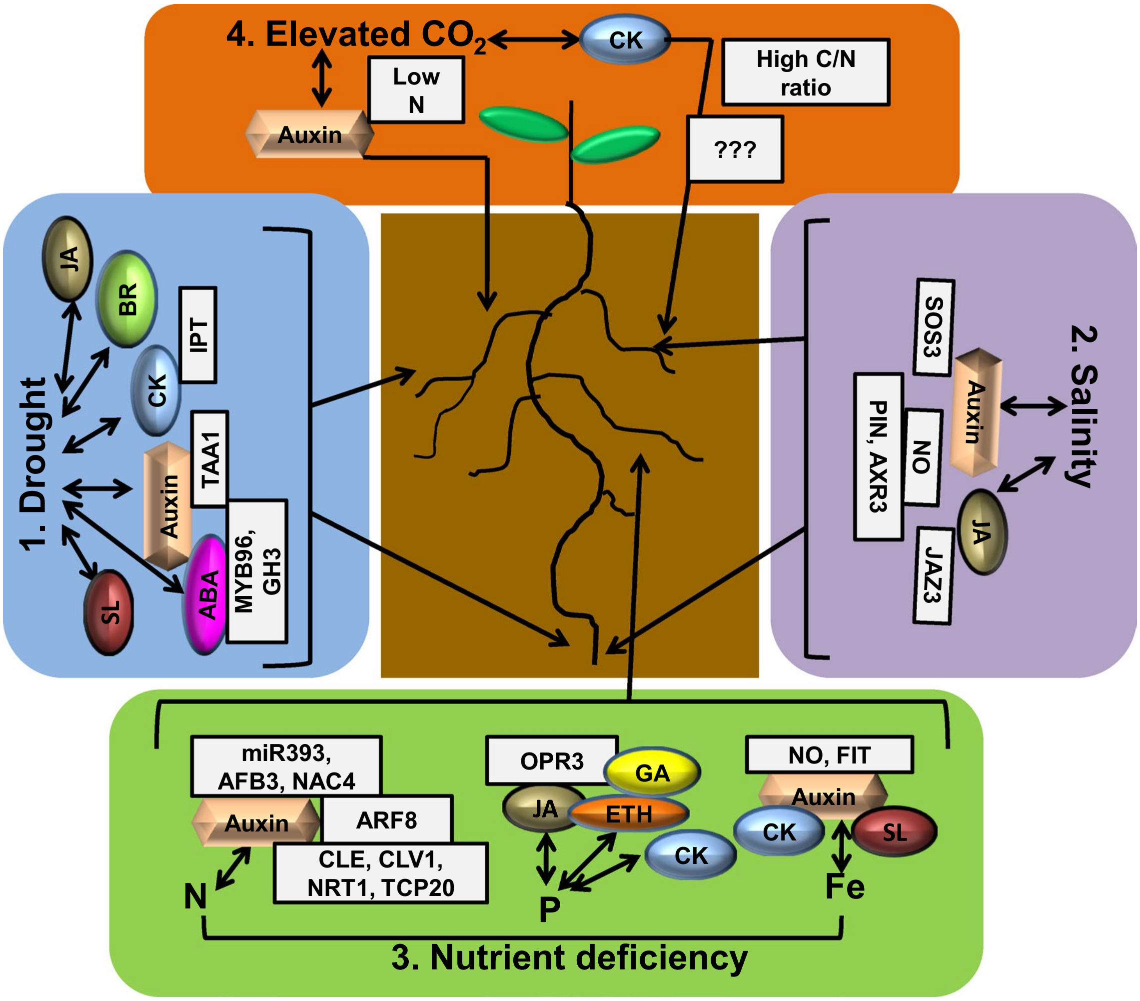

Fig. 2 Schematic representation demonstrating important hormone–environment interactions linked via some key downstream regulators in mediating RSA plasticity in general. *ABPs* actin binding proteins, *CLE* CLAVATA3/EMBRYO SURROUNDING REGION peptide, *DRO1* deep rooting 1, *HY5* like long hypocotyls 5, *miR160* micro RNA160, *TAA1* tryptophan aminotransferase of Arabidopsis 1

Integration of environmental and hormonal signals and key downstream regulators in RSA modulation

When comes to integration of external signals for modulating plant development, auxin comes first in the cue. Two interesting reviews have discussed how auxin mediates the integration of various environmental signals for modulating RSA as well as plant development as a whole. However, most of the reports on identification of downstream regulators are at their incipient stages and detailed mechanisms for each interacting pathways for RSA modulation requires further research. A consolidated list of inter-hormonal as well as hormone–environmental crosstalks affecting different components of RSA through some key downstream regulators is provided in Table 1.

Downstream to hormones, small signalling peptides and receptor like kinases are now recognized as potential mediator for RSA modulation. The best example is the CLE peptide which was proved to interact with auxin signaling pathway and play a crucial role in RSA modulation of both dicots and monocots. It was observed that CLE26 effect is mediated via auxin pathway as the CLE26 peptide alters the distribution of auxin in the root apical meristem by post-translational downregulation of PIN1 and also indirectly by repressing protophloem development (Czyzewicz and De Smet 2016). Now, CLE peptides are also reported to be cytokinin and N responsive (Araya et al. 2014; Marhavy et al. 2014) which provides an indication that these group of peptides acts as a common downstream regulator which

Table 1 An overview of recently deciphered inter-hormonal and hormone–environmental crosstalk, involved in modulating different components of RSA with their respective key downstream regulators

RSA component	Hormones	Downstream regulators	Key references
Inter-hormonal crosstalk			
Root meristem	Auxin–CK	PIN7, ARR7, ARR15, ARR1, SHY2, PRL1, WOX5, PLT1, PLT2	Dello Ioio et al. (2008), Ji et al. (2015), Su et al. (2011)
	Auxin–CK–GA	ARR1, ARR2, SHY2, RGA	Depuydt and Hardtke (2011), Shani et al. (2013)
	ETH–auxin–CK	SHY2	Street et al. (2015)
	Aux–JA	JAZ, MYC2, PLT1, PLT2	Chen et al. (2011), Kazan and Manners (2012)
Root hair	Aux–ETH	AUX1, ACS	Jones et al. (2009), Muday et al. (2012)
	ETH–BR	BRI1, BES1/BZR2	Fridman et al. (2014)
Lateral roots	ETH–CK	PIN1, PIN2, PLS	Liu et al. (2013, 2013)
	ETH–auxin	ACC, ACS	Lewis et al. (2011)
	SL–CK	AHK3, ARR1, SHY2	Jiang et al. (2016)
	ABA–auxin	FCA	De Smet et al. (2006)
	SL–auxin	GSH, MAX2	Cheng et al. (2013), Marquez-Garcia et al. (2014)
Root angle	Auxin–gravity	DRO1	Uga et al. (2013)
Hormone–environment interaction			
Lateral root (FC) initiation	Drought–auxin	TAA1	Bao et al. (2014)
Primary and lateral root growth	Drought–CK/JA/BR	IPT	Peleg et al. (2011)
Root meristem	Drought–auxin/ABA	MYB96, GH3	Seo and Park (2009)
Root adaptation	Drought–SL	Not yet identified	Visentin et al. (2016), Pandey et al. (2016)
RMC and primary root growth	Salinity–JA	JAZ	Geng et al. (2013)
Root meristem maintenance	Salinity–auxin	NO, PIN, AXR3	Liu et al. (2015)
Lateral root growth, root hair	Salinity–auxin	SOS3	Zhao et al. (2011)
Lateral root growth and development	N deficiency–auxin	CLE, CLV1 receptor like kinase, ANR1, ARF8, TCP20	Guan et al. (2014), Araya et al. (2014), Vidal et al. (2013), Wang et al. (2015)
Primary root growth	P deficiency–JA	OPR3	Zheng et al. (2016)
Primary and lateral root development	Fe deficiency–auxin/CK/SL	NO, FIT	Wu et al. (2012), Chen et al. (2010)
Primary and lateral root growth	CK-elevated CO_2–N deficiency	Not yet identified	Yong et al. (2000), Hachiya et al. (2014)

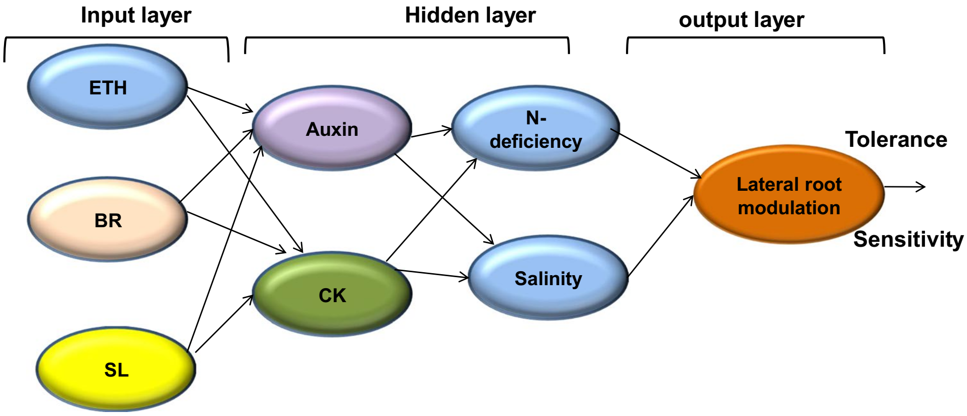

Fig. 3 A hypothetical model illustrating the possibility of utilizing ANN technology for selecting the best RSA modulating factors under specific adverse environmental conditions

integrates both inter-hormonal crosstalks as well as hormone–environmental interactions with respect to RSA plasticity. Lateral root induction was found to be significantly promoted in Arabidopsis through heterologous expression of a chrysanthemum LATERAL ORGAN BOUNDARY DOMAIN (CmLBD1) transcription factor which acts as a positive regulator of auxin signaling pathway for lateral root development (Zhu et al. 2016). On a similar note, a root exudates component methyl 3-(4-hydroxyphenyl)propionate (MHPP) was shown to modulate RSA via auxin and NO/ROS signaling pathways (Liu et al. 2016).

Due to the involvement of apparently complex interactions plant responses such as RSA plasticity were often found to be difficult to be analyzed through simple mathematical models and step wise algorithms. Thus, a much efficient yet simple alternative technology, artificial neuronal network (ANN) has been proposed by Gago et al. (2010a) to describe how sugar concentration and light intensity influences the in vitro explant proliferation of kiwifruit in tissue culture. The above approach of using ANN technology to select the best condition for in vitro explants proliferation by taking into consideration the interactive effects of two of the most crucial factors, i.e., sugar and light is highly encouraging for plant biologists as mathematical specialization is not required and it is reported to provide an overall view of the experimental study with only limited experimentation (Gago et al. 2010b). Though a bit speculative at present but as more reports on the mechanism as well as regulation of downstream regulatory components with respect to RSA modulation comes up, it is not impossible to start utilizing ANN networking software for selecting the best interactive partners (inter hormonal as well as hormone–environment) yielding a highly optimized RSA modulation under specific stress conditions. An interesting review by Gallego et al. (2011) on utilizing ANN technology for predicting biological processes, has promptly discussed the advantages of ANN technology over traditional statistical methods for analyzing and integrating the complex, non-linear biological data inputs. As ANN technology could capture non-linear relationships and external factor effects, we believe developing an ANN network of different hormone–environment interaction pattern modulating specific RSA component would be possible. Further, such ANN networks could be extended to genetic algorithms by using the "IF, THEN" rule to predict different RSA responses (Gallego et al. 2011). Despite initial obstacles of designing such networks, such an approach could provide novel concepts on how plants integrate large number of external and internal signals and channel them towards a common output in the form of specific modulation of RSA components. A hypothetical and simplified ANN model for such an approach to analyze the effect of different hormonal and environmental crosstalks using regular experimental data has been illustrated in Fig. 3.

Gaps and challenges encountered at present

At present, we can clearly visualize that after shoot biomass and seed yield, targeting RSA modulation is the next upcoming strategy for increasing productivity under adverse environmental conditions. Flow of information on regulation of RSA traits via hormone–environment interacting networks is also extensive. However, the major gap between the current information regarding factors affecting RSA and the application of this information on actual crop improvement program is the inefficiency in transferring the Arabidopsis model related mechanisms to actual field grown crops. On one hand it is exciting to uncover a new set of downstream regulators integrating the diverse hormonal and environmental signaling networks regulating the RSA but on the other hand, we are still restricted for a common interface giving information on key molecular targets involved in enhancing RSA traits towards better adaptation under adverse climatic conditions. Though the entire inter hormonal and hormone–environment crosstalks appears highly complicated and diverse, if a close integrated insight is taken up for targeting a common phenotypic output such as RSA modulation (as attempted in the present review article), a coordinated and well organized network could be presented. Further, a multidisciplinary approach by involving biologists, mathematicians and bioinformaticians to work together and come out with simple models, databases and softwares (based on ANN) for providing easy accessibility and understanding of different hormone–environment signals affecting specific RSA components via some specific downstream regulators is highly required.

Future research prospects

Hormone–environment signaling integration, through key mediators is still at its juvenile stage and needs further research complementation. For example, how specific nutrient signals regulate alteration in specific RSA components and the signals are mediated through which downstream regulators. Further, similar to hydropatterning, whether nutrient availability around the root circumference also plays a role by interacting with certain hormonal factors in shaping the lateral root emergence, i.e., a phenomenon like "Nutripatterning" exists or not, requires further research inputs in this aspect. Also, in line with the present climate change issues, it is highly crucial to dissect the signaling pathways mediating the elevated CO_2 induced RSA plasticity in both legumes and non-legumes. Finally, more key downstream regulators like CLE peptide needs to be identified to bridge the gap between hormone–environment signaling pathways and RSA modulation. Hence, the recent trend for thorough understanding of the RSA modulating regulatory factors opens up a huge avenue for research specifically targeting the hidden sphere of the plant system.

Acknowledgements Present work is supported by the Science and Engineering Research Board (Department of Science and Technology) Young Scientist Start Up Grant (YSS/2015/000635) to DS.

Compliance with ethical standards

Conflict of interest Authors declare no conflict of interest.

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