



Review On Phytohormones signaling cross-talk: to control plant growth and development

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Abstract

Phytohormones are natural chemical messengers that play critical roles in the regulation of plant growth and development as well as responses to biotic and abiotic stress factors, maintaining plant homeostasis, and allowing adaptation to environmental changes. In contrast to animals, plants can continuously cease and resume growth and development. This flexibility in their architecture and growth and development patterns is partly achieved by the action of plant hormones. Plant hormones are structurally diverse compounds that act usually at nanomolar concentrations and include different groups of the so-called “classic” hormones, namely auxins, cytokinins, gibberellins, abscisic acid, and ethylene. Jasmonates, salicylates, strigolactones, brassinosteroids, polyamines, and some peptides were recognized as new families of plant hormones. Hormones build a signaling network and mutually regulate several signaling and metabolic systems, which are essential both for plant development, growth and plant responses to biotic and abiotic stresses. Plant hormones can exert strong, seemingly independent actions on plant growth and development. Auxin generally promotes growth; cytokinins delay leaf senescence and influence cell division; abscisic acid causes bud dormancy and promotes stomatal closure; gibberellins function in seed germination, and so on. Of course, in reality, these hormones exert many of their effects through a complex series of interactions with other hormones and signaling molecules. In this review, we focus our attention on the signaling cross talk on phytohormones in plant growth and development. Therefore, the integration of various external signals with endogenous developmental programme is essential for their growth and development process.

Keywords: Crosstalk, Development. Growth, Light, Phytohormones , Temperature,

1. Introduction

1.1 Background of the review paper

This review paper highlights the signaling crosstalk among phytohormones, light and temperature which are essential for plant growth and development. Plant growth and development are controlled by both external cue and intrinsic growth regulators, such as

hormones. Mounting evidence suggests that environmental cues target the biosynthesis or perception of hormones, which therefore not only orchestrate intrinsic developmental programs, but also convey environmental inputs. All of them have been linked to growth regulation in one way or another, sometimes in a context-specific manner.

A plant's survival relies on its ability to adapt to the constantly changing environment. Unlike animals, plants cannot leave unfavorable conditions, so they have evolved a network of sophisticated mechanisms to perceive and properly respond to their surroundings. To stay in tune with their environment, plants constantly adjust their growth and development by manipulating a limited set of phytohormones. These compounds are then used in a combinatorial way to produce a wide variety of specific responses, dependent not only on the types of stimuli sensed, but also on the developmental stage and tissue type (Bennett et al., 2005).

Plants are sessile organisms and therefore must adapt their growth and architecture to a changing environment. Hormone signaling systems coordinate plant growth and development through a range of complex interactions. The original "classical" plant hormones are ethylene, cytokinin, auxin, abscisic acid (ABA), and gibberellins (GAs); more recently identified hormones include brassinosteroids, strigolactones, salicylic acid, nitric oxide, and jasmonic acid (Santner and Estelle, 2009).

Plants are also that have to readily alter their development and growth responses to survive an ever changing environment. This involves the correct amalgamation of multiple external signals including temperature and light, in all aspect of development, from germination to flowering. Temperature is an environmental factor that has a considerable influence throughout the plant's developmental program. It plays a major role in controlling the degree of seed dormancy (Koornneef *et al.*, 2002).

Plant hormones play a crucial role in controlling the way in which plants grow and develop. While metabolism provides the power and building blocks for plant life, it is the hormones that regulate the speed of growth of the individual parts and integrate these parts to produce the form that we recognize as a plant (Gaspar *et al.*, 2002).

Plant hormones can exert strong, seemingly independent actions on plant growth and development. Auxin generally promotes growth; cytokinins delay leaf senescence and influence cell division; abscisic acid causes bud dormancy and promotes stomatal closure; gibberellins function in seed germination, and so on. Of course, in reality, these hormones exert

many of their effects through a complex series of interactions with other hormones and signaling molecules (Nancy A. Eckardt, 2015).

At least seven groups of phytohormones have been well characterized, including abscisic acid (ABA), auxin, brassinosteroid (BR), cytokinin (CK), ethylene, gibberellin (GA), and jasmonate (JA). A central feature of plant development is the largely postembryonic formation of the plant body. While in animals practically all organs are formed during embryogenesis and elaborated during the juvenile stage, plant embryogenesis results in the formation of a miniature plant. This so called seedling possesses discrete stem cell pools in the shoot and root meristems, which form the vast majority of plant organs post embryonically in a modular, reiterative fashion that also integrates environmental inputs (Wang and Dong, 2011).

It has always been clear that different plant hormones affect overlapping processes, such that the output of plant hormone action depends on specific hormone combinations rather than on the independent activities of each. In the last two decades, numerous components of the signal transduction pathways of various plant hormones have been identified, leading to the elucidation of partial or entire signaling cascades (Bouquin et al., 2001)

Plant hormone crosstalk is a complex topic of broad and current interest. In this review, we provide a comprehensive overview of the interaction of different plant hormone during plant development and growth. I hope that this review paper in this special issue will allow readers to gain a better understanding of various phytohormones, light and temperature which interact to control plant growth and development and also summarized the recent exciting progress in hormone signaling cross talk and other a biotic factor.

2. Literature Review

2.1 Phytohormonal signaling cross talk in plant growth and development

2.1.1 Auxin signaling cross talk

Auxin cross talk with other signaling molecules was originally studied by observing the effects of

exogenous application of combinations of hormones on plant proliferation or morphology (Skoog and Miller, 1957). As endogenous factors, hormones play an indispensable role in regulating the developmental processes. Hormonal regulation of development is a complex processes with interaction so various hormones at transcriptional, translational and cellular levels (Chandler, 2009). Among the hormones, auxin (indole-3-acetic acid, IAA), the first discovered plant hormone, controls essentially all aspects of plant development, from embryogenesis to senescence (Davies 1995). In addition, auxin also plays a central role in the existing hormonal crosstalk, which influence various developmental stages (Swarup et al. 2002, Chandler 2009, Depudyt and Hardtke 2011) Fig 1. It influences cell division, cell elongation and programmed cell death, driving embryonic and post embryonic development (Davies, 2004). The effect of auxin is dependent on cell type: at the same concentration, indole-3-acetic acid (IAA) simultaneously stimulates hypocotyl elongation, suppresses main root growth, induces lateral root initiation, and stimulates root hair formation.

Auxin and cytokinin have been shown to act both synergistically and antagonistically for shoot and root development, respectively (Swarup et al. 2002, Dello Ioio et al. 2008). Another set of hormones that have classic and complex interaction is auxin and ethylene. They show both synergistic and antagonistic interactions in regulating various developmental processes, such as apical hook formation, root and shoot elongation, root and shoot gravitropism, lateral root development, root hair initiation and elongation, hypocotyl phototropism and leaf abscission (Muday et al. 2012). Gibberellin (GA) and auxin have been shown to coordinately regulate pea stem elongation and parthenocarpy (Swarup et al. 2002), lateral root development in populus (Gou et al. 2010) and apical

dominance, inflorescence and root development in Arabidopsis (Silverstone et al.1997, Willige et al.2011). Brassinolide (BR) interacts with auxin to regulate the cell elongation process in root, shoot and tropisms (for review, see Hardtke et al. 2007). Jasmonic acid (JA) and auxin act synergistically to regulate root growth, lateral root development and flowering, while they act antagonistically in regulating the coleoptile elongation (for review, see Chandler 2009). Recent reports suggest that ABA and auxin interact in regulating the lateral root development (Shkolnik-Inbar and Bar-Zvi 2010). Auxin is unique among the plant hormones with its capacity to move both long and short distances. The long-distance transport is rapid and source-to-sink type, where auxin moves from biosynthetically highly active young tissues to sink tissue such as root through phloem (Marchant et al., 2002). The short-distance transport is slower, occurs in a cell-to-cell manner and is regulated by specific influx and efflux carrier proteins (Muday and Rahman 2008). Proteins belong to AUX/LAX and PIN families act as major regulators of cellular auxin transport by facilitating the influx and efflux, respectively. In Arabidopsis, two polar transport streams function in facilitating the intracellular auxin transport. The unidirectional transport from shoot apex to root, rootward auxin transport, is regulated by PIN1 (Geldner et al. 2001). In the root, auxin transport is more complex, with two distinct polarities (Abidur Rahman , 2013). In the root, auxin transport is more complex, with two distinct polarities. IAA moves toward the root tip (rootward direction), through the central cylinder cells with the aid of AUX1, ABCB19 and PIN1,3,7 (for review, see Muday et al. 2012). Once it reaches the root tip, IAA moves in a reverse direction toward the shoot through the outer layers of root cells. This shootward movement of IAA is regulated by AUX1, PIN2 and ABCB4 (for review, see Peer et al. 2011).



Fig. 1. Hormonal crosstalk regulating the plant growth and development, auxin at center.

Auxin and cytokinin play fairly important roles in many aspects of plant growth and development (Eklof et al., 2000). The interaction between auxin and cytokinin is particularly important to control a few developmental processes, such as the formation and maintenance of meristems that are essential to establish the whole plant body. For example, the shoot meristems give rise to the above-ground parts of a plant, whereas the root meristems produce the below-ground parts. Thus, phytohormones auxin and cytokinin (CK) control major cell specification events, stimulate growth and are present during embryogenesis and seedling establishment (Bennett and Scheres, 2010; Perilli et al., 2010). Many recent studies have provided important information for the understanding of the molecular mechanisms of auxin–cytokinin interaction in the regulation of meristem development (Ying-Hua Su, 2011). Studies on *Arabidopsis* and other plant species have revealed the roles of auxin and cytokinin in the formation of lateral roots (LR). Physiological and genetic data have demonstrated that auxin promotes LR initiation and lateral root primordium (LRP) development (Fukaki and Tasaka, 2009; Peret et al., 2009).

Several studies have shown that cytokinin and auxin mutually regulate their signaling pathways or their metabolisms through certain integrators, which are the basis of interaction between these two hormones to

determine a specific developmental output in root meristem (Dello Ioio et al., 2008; Moubayidin et al., 2009; Ru'z'ic'kaa et al., 2009). Recently, a genetic framework has shown that antagonistic interaction between cytokinin and auxin is responsible for the control of cell division and cell differentiation in the root meristem (Dello Ioio et al., 2008; Moubayidin et al., 2009). There are multiple points of interaction between the auxin and cytokinin pathways. In addition to the inter-hormonal interactions shown, both hormones regulate their own metabolism and perception, adding further complexity to the pathways. Interactions between auxin and cytokinin are crucial for many important aspects of plant development (e.g. in shoot branching, the shoot meristem, the root transition zone, lateral root initiation and in the root meristem (Sedeer El-Showk *et al.*, 2013) Fig 2.

Cytokinins are also known to play a role in axillary branching in the shoot. Increased levels of strigolactones in pea and *Arabidopsis* lead to reduced cytokinin levels in the xylem sap, although levels in the shoot remain unchanged (Foo et al., 2007). Dun et al. (Dun et al., 2009) found that the buds of strigolactone-insensitive plants also have reduced sensitivity to cytokinin supplied from the vasculature. Cytokinin may also prevent auxin upregulation of MAX4, a strigolactone biosynthesis gene (Bainbridge et al., 2005) Fig 2.

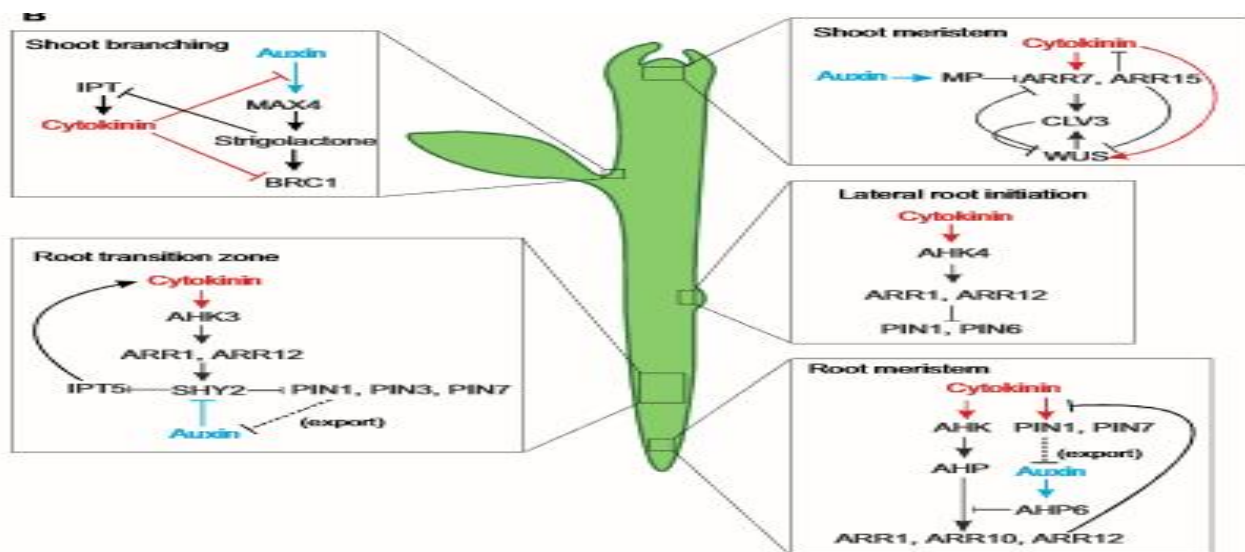


Fig. 2 . Auxin interacts with cytokinin in several developmental contexts.

There are multiple points of interaction between the auxin and cytokinin pathways (Sedeer El-Showk *et al.* 2013). Dello Ioio *et al.* therefore proposed a model in which the size of the root meristem is determined by an antagonism between auxin and cytokinin in the vascular transition zone; this antagonism is mediated by opposing regulation of SHY2, which in turn negatively regulates cytokinin biosynthesis while repressing auxin transport and signaling (Dello Ioio *et al.*, 2008) (Fig. 2). Further evidence that cytokinin modulates auxin transport by regulating PIN transporters came from a study by R ži ka *et al.* (R ži ka *et al.*, 2009). Cytokinin decreases the expression of PIN1 and PIN3 in the Arabidopsis root meristem while increasing the expression of PIN 7 (Kalousek *et al.*, 2010). In an elegant experiment, Müller and Sheen (Müller and Sheen, 2008) showed that auxin directly activates two type A ARR s, ARR7 and ARR15, thereby inhibiting cytokinin signaling (Zhang *et al.*, 2011 (Fig. 2)

Cytokinin regulation of PIN genes, SHY2 was also found to negatively regulate the cytokinin biosynthesis gene IPT5. Dello Ioio *et al.* therefore proposed a model in which the size of the root meristem is determined by an antagonism between auxin and cytokinin in the vascular transition zone; this antagonism is mediated by opposing regulation of SHY2, which in turn negatively regulates cytokinin biosynthesis while repressing auxin transport and signalling (Sedeer El-Showk *et al.* , 2013) (Fig. 2). The Aux/IAA SHORT HYPOCOTYL2 (SHY2) gene, a repressor of auxin signalling, has a crucial role in controlling meristem size and development (Elena Pacifici *et al.*, 2015).

Auxin and ethylene coordinately regulate several developmental programs in plants. For example, in Arabidopsis auxin and ethylene have been described to regulate apical hook formation (Raz and Ecker , 1999) root hair differentiation (Masucci and Schiefelbein, 1994) , root hair elongation (Pitts *et al.*, 1998), root growth (Rahman *et al.*, 2001) and hypocotyls phototropism (Harper *et al.*, 2000) .

In Arabidopsis thaliana multiple studies have shown that root elongation during early root development is inhibited by the gaseous plant growth regulator ethylene (Ruzicka *et al.*, 2007; Stepanova *et al.*, 2007; Swarup *et al.*, 2007; Markakis *et al.*, 2012). However, Pierik *et al.* (2006) have proposed a biphasic ethylene response model where ethylene has both an inhibitory and stimulatory effect on root elongation depending on the ethylene concentration and the species. Recently study show that early root growth in sugar

beet also shows a biphasic ethylene response (Abts *et al.*, 2014).

Application of low concentrations of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC) stimulates root growth while high concentrations inhibit root growth (Abts *et al.*, 2014). It is also known that auxin can inhibit root elongation in many species (e.g., Arabidopsis, Brassica, maize, pea...; Eliasson *et al.*, 1989; Rahman *et al.*, 2007; Ruzicka *et al.*, 2007; Stepanova *et al.*, 2007; Swarup *et al.*, 2007; Alarcón *et al.*, 2012; Polit *et al.*, 2014). In contradiction, it was also previously shown in Arabidopsis that low auxin levels could stimulate root elongation (Evans *et al.*, 1994) which might suggest that auxins can also exert a biphasic response in root growth. However, the auxin response during early root growth of sugar beet remains elusive (WILLEM ABTS *et al.*, 2017).

Studies in Arabidopsis have shown that ethylene stimulates auxin biosynthesis and upregulates the transcription of several auxin transporters (e.g., PIN1, PIN2, AUX1; Ruzicka *et al.*, 2007; Stepanova *et al.*, 2007; Swarup *et al.*, 2007).

In the current paper, Liu *et al.* (2018) reveal that ethylene–auxin cross-talk involves the active interaction between ERF.B3 and IAA27. The evidence they provide to support this is that the overexpression of a dominant repressor form of ERF.B3 results in altered auxin sensitivity, root development and an impaired chlorophyll accumulation in a manner reminiscent of the phenotypes of lines where the expression of IAA27 is downregulated . (Liu M *et al.* 2018)

Abscisic acid (ABA) and auxin have been observed to interact antagonistically to regulate stomatal aperture (Eckert and Kaldenhoff, 2000). Auxin causes a reduction in turgor within guard cells which concomitantly serves to open the stomatal pore. Conversely, ABA serves to increase turgor within guard cells thus closing the stomatal pore and reducing water loss via transpiration. The antagonistic nature of this interaction requires the precise coordination of ion channel activity within guard cells. These channels allow the flow of ions that decrease (auxin) or increase (ABA) the cytosolic pH and therefore effect the turgor of the guard cells (Grabov and Blatt, 1998). Aside from interactions of auxin and ABA at the level of guard cell aperture, genetic evidence from Arabidopsis

indicates these two hormones may interact to influence root growth and seed germination (Nagpal et al., 2000).

Crosstalk between BR and auxin regulates innumerable phases of plant growth and developmental routes (Hao J *et al*, 2013). Interactive effects of BRs and auxin involved physiological process such as hypocotyl elongation or root development. Additionally, auxin and brassinosteroids (BR) have been reported to coordinately regulate several plant developmental processes. For example, studies in monocotyledons have shown that auxin and BR positively interact to control lamina joint bending (Yamamuro et al., 2000).

JA, a fatty-acid-derived signaling molecule, is involved in several aspects of plant biology including pollen and seed development, and defense against wounding, ozone, insect pests and microbial pathogens (Barbara N Kunkel *et al*, 2002). Jasmonic acid (JA) is well known to promote lateral root formation but the mechanisms by which JA signaling is integrated into the pathways responsible for lateral root formation, and how it interacts with auxin in this process remains poorly understood (Xiao-Teng Cai1, 2014) . Notably, all of these hormones can regulate many processes singlehandedly and independently, but cooperation and crosstalk between their signalling pathways appear to exist, as deduced from their overlapping influence on various cellular processes Nemhauser *et al* , 2004) Fig 3

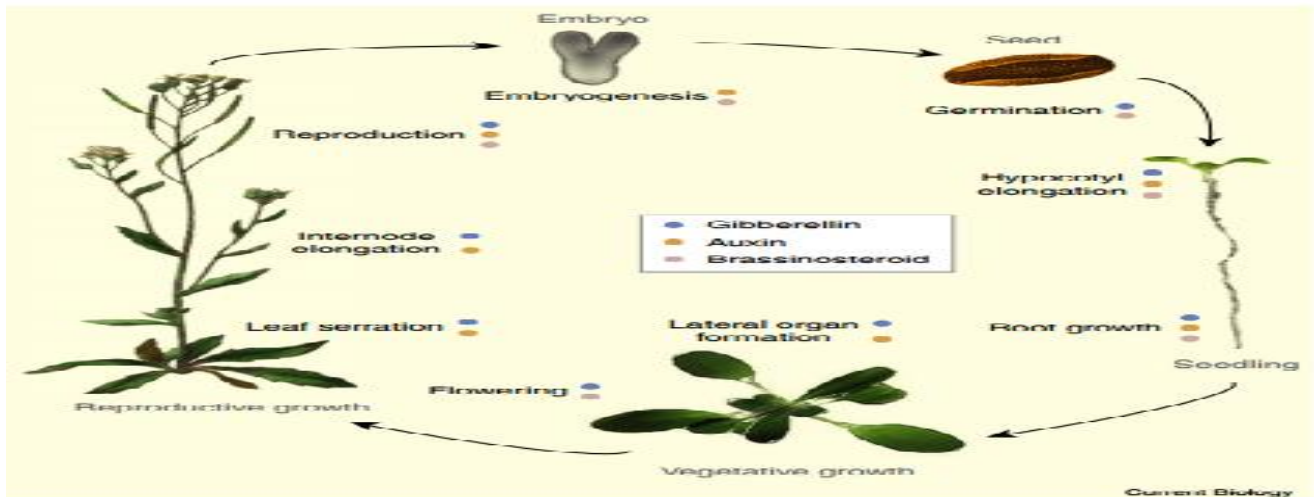


Fig 3. Examples of auxin, gibberellin or brassinosteroid involvement in growth phenomena Across the plant life cycle

2.1.2. Gibberellin signaling cross talk

Gibberellins have a major influence on germination, plant growth in general (mainly via cell expansion), floral development and flowering time. They control seed germination, leaf expansion, stem elongation and flowering (Magome et al., 2004). The mode of GA action in planta is still far from being understood, as numerous positive and negative functional interactions with other endogenous and environmental cues affect GA responses (Nemhauser et al., 2006) (Fig. 3).

Several genes encoding GA signalling components involved in seed germination are also known (Tyler et al., 2004). RGL2 negatively regulates GA responses that primarily control seed germination (Lee et al., 2002). The Arabidopsis gene SPY is also a negative regulator of GA signalling. However, unlike RGL2 it also regulates all other developmental processes involving GA (Izhaki et al., 2001). In addition, SPY is an activator of cytokinin signalling pathway (Greenboim-Wainberg et al., 2005).

2.1.2.1 Mechanism of the antagonistic interaction between GA and ABA

GAs regulates various developmental processes throughout the life cycle of the plant, from seed germination through leaf expansion, stem elongation,

flower induction and seed development (Sun and Gubler, 2004). As the interactions between GA and other hormones involve components from the GA biosynthetic and response pathways (Sun TP, Gobbler, 2004)

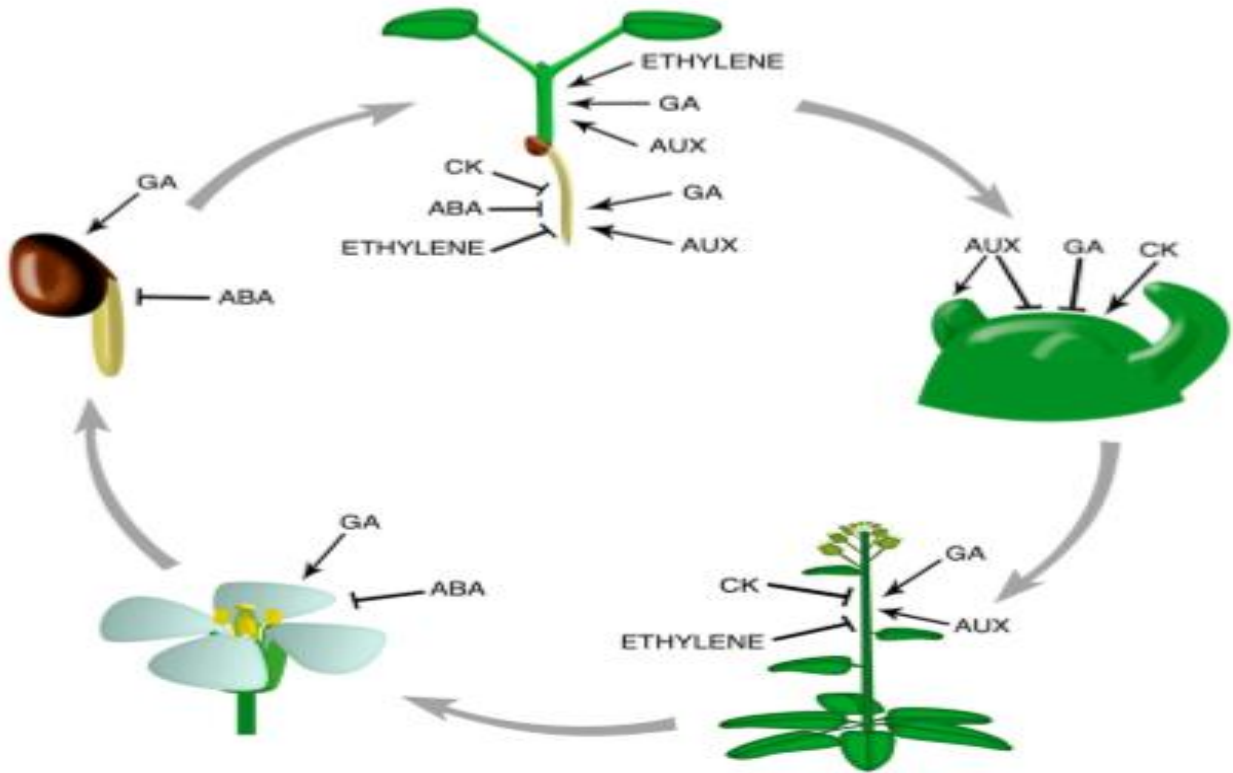


Fig. 4. GA interacts positively and negatively with other plant hormone throughout the Plant's life cycle.

GA and ABA play antagonistic roles in the regulation of numerous developmental processes. Whereas GA is associated with the promotion of germination, growth, and flowering, ABA inhibits these processes. Moreover, the antagonistic relationship and the ratio between these two hormones regulate the transition from embryogenesis to seed germination (Razem et al., 2006). Several different mechanisms have been shown to underlie this antagonistic interaction in different developmental processes (Fig 4). Among the photohormones that play a role in Arabidopsis seed germination, gibberellin (GA) and abscisic acid (ABA) have the most pronounced effects (Koornneef et al., 2002). ABA establishes and maintains dormancy of seeds, whereas GA has the opposite effect, breaking dormancy and inducing seed germination (Steber et al., 1998). A different mechanism of interaction between GA and ABA in the regulation of root growth was described by Achard et al. (2006). In Arabidopsis, GA promotes and ABA

suppresses root growth, and both effects seem to be mediated by the DELLA proteins (Xie Z *et al*, 2006).

The activities of GA and auxin overlap with respect to the regulation of cell expansion and tissue differentiation. Auxin affects GA signaling as well as GA biosynthesis (Fig. 4). In Arabidopsis, GA stimulation of root elongation has been shown to require auxin. GA-induced root elongation was inhibited by the removal of the shoot apex that is a major auxin source, and this effect was reversed by auxin application.

Ethylene inhibits growth in a GA-antagonistic manner have shown that at least part of the inhibitory effect of ethylene on growth and its interaction with GA in this regard is mediated by the DELLA proteins (Achard et al., 2007). GA promotes seedling root elongation in Arabidopsis, and this effect is inhibited by ethylene.

GA stimulated root elongation also in the presence of ethylene, suggesting that ethylene acts through these DELLA proteins in this process. GA promotes ethylene responses in dark- and light-grown seedling (apical hook formation in the dark and hypocotyl elongation in the light) (Achard et al., 2007).

Submergence promotes ethylene and GA synthesis in deep water rice and *R. palustris*, and GA promotes ethylene-induced internode elongation (Benschop et al., 2006). GAs are endogenous regulators of hypocotyl growth via cellular elongation through degradation of DELLA proteins in *Arabidopsis* (de Lucas et al., 2008).

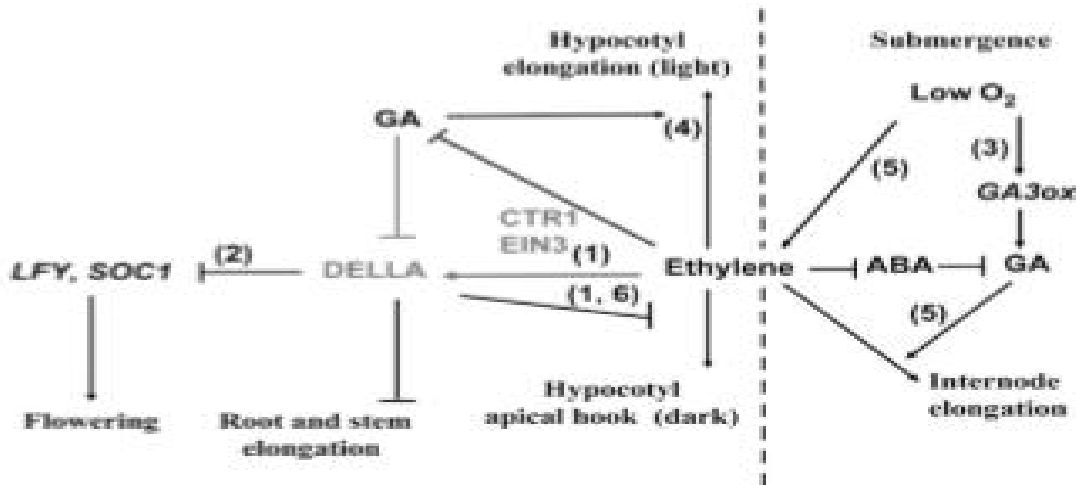


Fig 5. Network of positive and negative interactions between GA and ethylene.

Ethylene represses GA biosynthesis or suppresses GA responses via DELLA stabilization. Network of positive and negative interactions between GA and ethylene. Ethylene represses GA biosynthesis or suppresses GA responses via DELLA stabilization. GA promotes ethylene responses in dark- and light-grown seedling (apical hook formation in the dark and hypocotyl elongation in the light). Submergence promotes ethylene and GA synthesis in deepwater rice and *R. palustris*, and GA promotes ethylene-induced internode elongation. Interactions mediated by changes in protein activity or stability are in gray and those mediated by gene expression are in black. Numbers in parentheses indicate the respective reference as follows: 1, Achard et al., 2003; 2, Achard et al., 2007; 3, Benschop et al., 2006; 4, Sabio et al., 2003; 5, Sauter et al., 1995; 6, Vriezen et al., 2004. EIN3, ETHYLENE INSENSITIVE3; LFY, LEAFY; SOC1, SUPPRESSOR OF OVEREXPRESSION OF CONSTANS1.

2.1.3 Brassinosteroid signaling cross talk

Brassinosteroids (BRs) are a class of polyhydroxylated steroidal hormones playing

pivotal roles during many aspects of plant growth and development, such as cell elongation, cell division, senescence, vascular differentiation, reproduction, photomorphogenesis, and responses to various stresses (Clouse and Sasse, 1998; Divi and Krishna, 2009). Brassinosteroids have been reported in almost all plant tissues, with highest levels found in seeds, pollen and young growing tissues (Stephen Depuydt and Christian S. Hardtke, 2011).

Brassinosteroids act largely post embryonically with pronounced effects on general plant growth via cell elongation, vascular differentiation, and reproductive development (Pacifi *et al.*, 2015). Recent detailed analyses, revealed that BRs are not only involved in root cell elongation but are also involved in many aspects of root development, such as maintenance of meristem size, root hair formation, lateral root initiation, gravitropic response, mycorrhiza formation, and nodulation in legume species (Wei Z. and Li J, 2016).

2.1.4 Ethylene signaling cross talk

ET, a gaseous phytohormone, is involved in several phases of plant growth and development, notably fruit ripening, flower senescence, and leaf and petal abscission, besides being an essential regulator of stress responses. It is biosynthesized from methionine via S-adenosyl-L-methionine (*adomet*) and the cyclic non-protein amino acid ACC. ACC synthase converts S-adenosyl L-methionine to ACC, whereas ACC oxidase catalyzes the conversion of ACC to ET (Shabir H. Wani *et al*, 2015)

Ethylene enhances auxin transport in the root elongation zone by stimulating AUX1 and PIN2, leading to reduced cell elongation and root growth (Ruzicka *et al*. 2007), which is confirmed at the genetic level as both the *aux1* and *eir1/pin2* mutants are resistant to ethylene-induced root growth inhibition (Rahman *et al*. 2001). On the other hand, in mature region of root, ethylene inhibits AUX1 expression but stimulates PIN3 and PIN7, resulting in blocking the formation of auxin gradient required for lateral root development (Lewis *et al*. 2011). Ethylene-induced increase in apical curvature has also been attributed to an increase in auxin level modulated by the enhanced expression of PIN3 and AUX1 (for review, see Muday *et al*. 2012).

Auxin biosynthesis, transport, and signaling proved to be important for ethylene-induced hypocotyl growth in the light (Fig. 6). Auxin accumulation was enhanced by ethylene, concomitant with an increased expression of the auxin biosynthesis genes YUCCA1 and YUCCA5 (Bram Van de Poel *et al*, 2015)

Ethylene biosynthesis begins from methionine via S-adenosyl L-methionine and the cyclic amino acid ACC. ACC synthase converts S-adenosyl L-methionine to ACC, whereas ACC oxidase catalyzes the conversion of ACC to ET (Mohamed A. El Esawi, 2017)

Few reports have addressed the role of ethylene on cell division, revealing opposite actions on the cell cycle, depending on tissue type and internal and external cues. Ethylene stimulates cell division in the sub-epidermal layers during apical hook development, probably acting in cooperation with auxins (Raz and Koornneef, 2001).

Although ethylene is best known for its inhibition of cell elongation both in dark-grown seedlings (as part of the triple response; Bleecker *et al*., 1988; Guzmán and Ecker, 1990) and in light-grown plants (Rodrigues Pousada *et al*., 1993), there are several observations of ethylene-stimulated cell elongation. For example, ethylene induces cell elongation in the hypocotyl of seedlings grown in the light (Smalle *et al*., 1997) as well as root hair elongation (Pitts *et al*., 1998) and petiole elongation in certain ecotypes (Millenaar *et al*., 2005).

The effect of the plant hormones on elongation and their interaction often differ between light and darkness. Ethylene plays an important role in the regulation of hypocotyl development, in the light and presumably also in darkness, interacting with other plant hormones (Liang *et al*., 2012). Ethylene regulates hypocotyl growth both in light and in darkness. In the dark, ethylene inhibits, whereas in the light, it promotes, the growth of Arabidopsis hypocotyls (Lau and Deng, 2012) (Fig. 6)

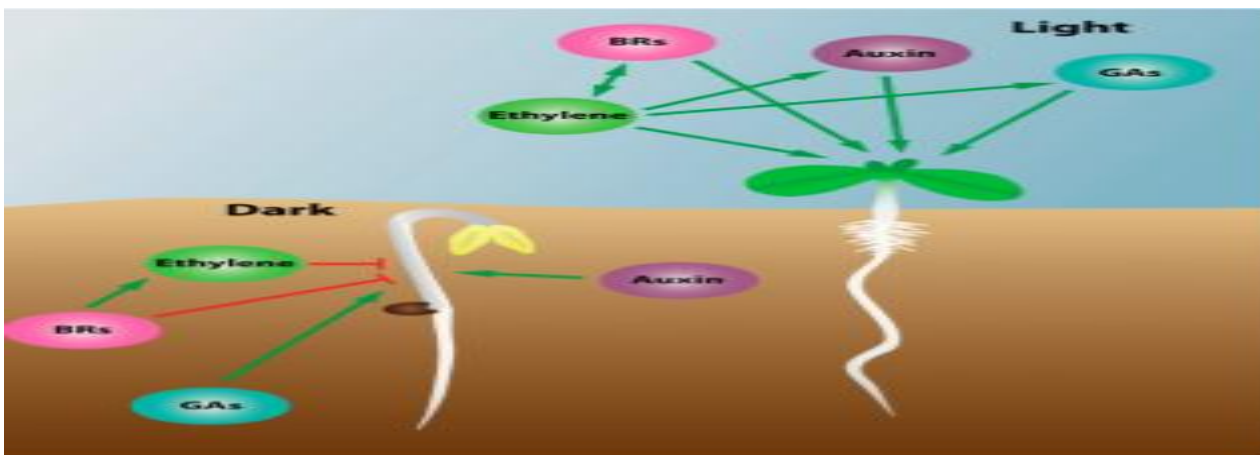


Fig 6. Simplified cross talk diagram showing the effects of and interactions between plants Hormones in the regulation of hypocotyl development.

Ethylene and brassinosteroids (BR) are also believed to play important roles in fruit set (Fu et al., 2008; Serrani et al., 2008; Wang et al., 2009). Recent evidence in *Arabidopsis* suggests that ethylene is involved in both the control of the ovule lifespan and the determination of the pistil/fruit fate. Ethylene and other phytohormones have been suggested to crosstalk to each other in the regulation of various aspects of plant development (Lin et al., 2008a; Santisree et al., 2011). The involvement of several plant growth regulators in fruit development and ripening indicates the possibility of an intricate hormonal co action module (Osorio et al., 2011).

2.1.5 Cytokinins signaling cross talk

Cytokinins are a major class of plant hormones that are involved in various aspects of plant development, ranging from organ formation and apical dominance to leaf senescence (Sedeer El-Showk, 2013). Cytokinins (CKs) regulate several plant growth aspects and developmental processes, including cell division, apical dominance, chloroplast biogenesis, nutrient mobilization, leaf senescence, vascular differentiation, photomorphogenic development, shoot differentiation and anthocyanin production (Mok and Mok, 2001; Davies, 2004). CKs are often considered as ABA antagonists and auxins antagonists/synergists in various processes in plants (Pospisilova, 2003). CKs retard senescence having effect on membrane permeability to mono and divalent ions, and localized induction of metabolic sinks (Letham, 1978). Early work on cytokinins showed that they promote shoot growth, inhibit root growth, stimulate cell division and induce greening in calli (Miller et al., 1956).

Cytokinin and gibberellin signalling come together in the regulation of ARR1, the expression of which is repressed by gibberellin (via degradation of the DELLA protein RGA, which promotes ARR1 expression) and promoted by cytokinin. The regulation of SHY2 by ARR1 also represents a point of crosstalk with auxin, thus connecting three hormones in one network (Moubayidin et al., 2010).

Cytokinin and Ethylene signalling converge in the control of the type A ARRs ARR5, ARR7 and ARR15, which play a role in freezing tolerance. Cytokinin also increases ethylene biosynthesis by increasing the stability of ACS proteins, which catalyse the rate-limiting step in ethylene biosynthesis (Chae et al., 2003).

Abscisic acid (ABA) is a plant hormone involved in seed dormancy, growth inhibition and stress response. Though not much is known about the interaction between cytokinin and ABA, several experiments have indicated that crosstalk occurs (Fig. 7C). Microarray and RT-PCR experiments demonstrated that CKX1, CKX3, CKX4 and CKX6 are downregulated by ABA (Werner et al., 2006). The final step involves catabolic genes that ensure the maintenance of a correct concentration of active cytokinin. Enzymes encoded by the CYTOKININ OXIDASE (CKX) gene family (Schmulling et al., 2003) mediate cytokinin degradation. Cytokinin signalling system interacts with abscisic acid (ABA), regulating salinity and drought response. ABA represses several CKX genes, whereas AHK2 and AHK3 downregulate many ABA-responsive genes (Jeon et al., 2010).

Strigolactones originally identified from branching mutants of *Arabidopsis thaliana*, *Pisum sativa* and other plants, strigolactones are thought to be produced mainly in the roots and to be transported upwards in the xylem to inhibit bud outgrowth (Beveridge, 2006; Kohlen et al., 2011).

Increased levels of strigolactones in pea and *Arabidopsis* lead to reduced cytokinin levels in the xylem sap, although levels in the shoot remain unchanged (Foo et al., 2007). Cytokinin interacts with strigolactones to regulate the outgrowth of axillary buds. In addition to inhibiting the transcription factor BRC1, which acts downstream of strigolactones, cytokinins prevent auxin-mediated regulation of the strigolactone biosynthesis gene MAX4. Strigolactones, in turn, negatively regulate cytokinin biosynthesis through IPT1 (Dun et al., 2009)

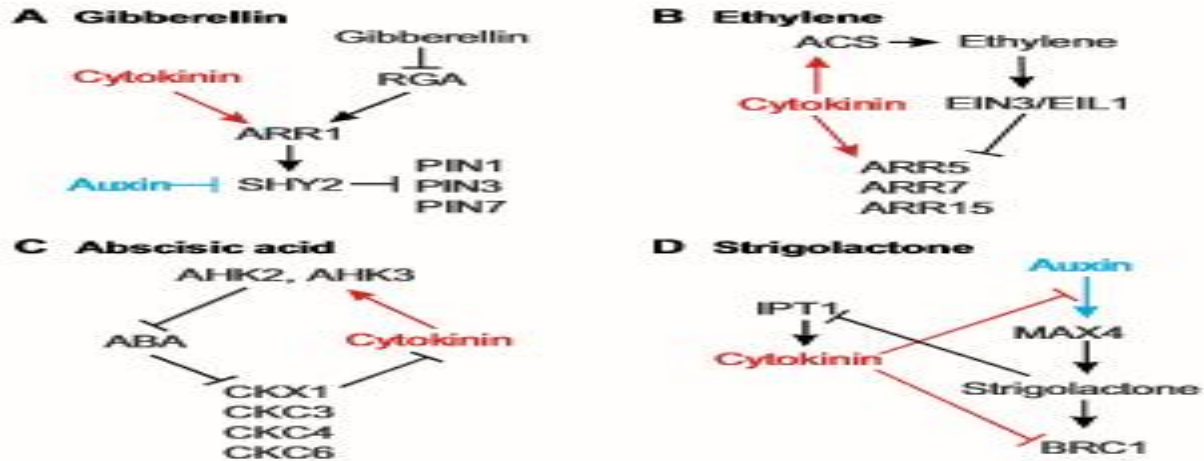


Figure 7: Interaction between cytokinin and other hormones

2.1.6 NO signaling cross talk

NO is one of the first signaling cues being produced after auxin, ABA, GAs or CKs addition. This molecule is involved in the regulation of plant growth and development, pathogen defense and abiotic stress responses, and in most cases this is achieved through its interaction with phytohormones (Luis Sanz, 2015). NO is the most abundant reactive nitrogen species (RNS) in plants. NO as a signaling molecule usually interacts with plant hormones and other endogenous molecules during early growth and development of plants (Freschi, 2013) (Fig. 1). NO can break seed dormancy in Arabidopsis and barley while the NO scavenger 2-(4-carboxyphenyl)-4, 4, 5, 5 tetramethyl imidazoline-1-oxyl-3-oxide (cPTIO) effectively promotes the maintenance of seed dormancy (Bethke et al., 2004b, 2006a). These findings suggested that NO is an endogenous regulator of seed germination in these species (Sarath et al., 2005). NO is involved in the promotion of seed germination, photomorphogenesis, mitochondrial activity, leaf expansion, root growth, stomatal closure, fruit maturation, senescence and iron metabolism (Neill, 2007).

ABA plays a key role during the induction and maintenance of seed dormancy, the inhibition of seed germination and later post-germination developmental checkpoints (Finkelstein, 2013). Conversely, NO acts as a dormancy-relieving molecule and promoter of seed germination (Bethke et al., 2004b). NO induces dormancy breakage and stimulates germination of apple embryos by induction of ET biosynthesis (Gniazdowska et al. 2007). Most evidence suggests that NO acts downstream of auxin in planta (Chen et al., 2010), NO reduces auxin degradation by inhibiting IAA oxidase activity (2: Xu et al., 2010). Enhanced NO levels inhibit auxin transport in Arabidopsis roots NO is involved in Arabidopsis root hair formation in both the initiation and elongation phases (Lombardo et al., 2006). CKs are key hormones that regulate root development, its vascular differentiation and root gravitropism. CK addition reduces primary root growth and meristem length by stimulating the expression of SHY2 through ARR CK-responsive transcription factors, which are also stimulated by the RGA DELLA protein (Romanov et al., 2008) Fig 8 . Auxin increases NO production under certain stresses such as iron deficiency (Chen et al., 2010)

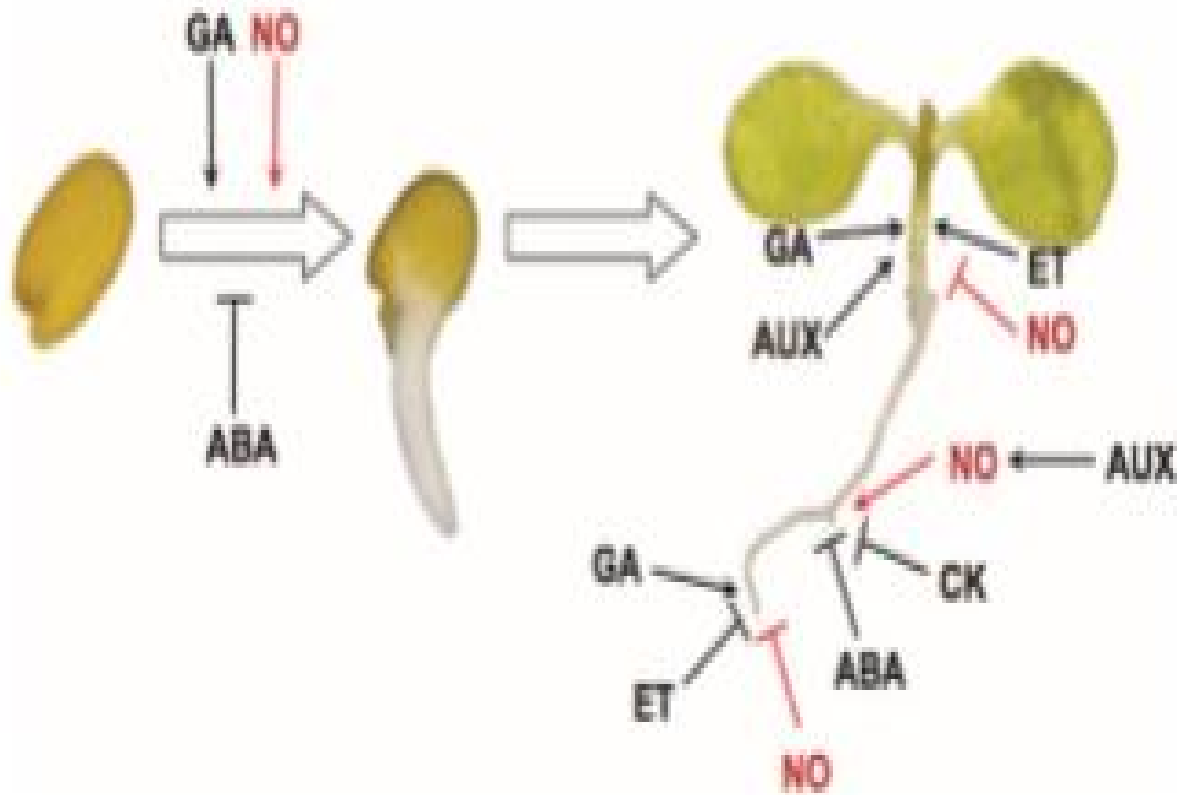


Fig 8 Schematic representation of the physiological NO role in Arabidopsis seed Germination And early seedling development together with the different phytohormones.

GAs is endogenous regulators of hypocotyl growth via cellular elongation through degradation of DELLA proteins in Arabidopsis (de Lucas et al., 2008). NO is a central signaling molecule with several effects on control of root architecture. Recently, Feng et al. (2013) demonstrated that NO represses CK signalling by inhibiting the phosphorelay activity through S-nitrosylation of the histidine phosphotransfer protein AHP1.

2.1.7 Light signaling cross talk

As sessile organisms plants that cannot choose their surroundings, plants need to modify their growth and development to suit their ambient environment. Such developmental plasticity involves the integration of multiple environmental signals, enabling plants to synchronize their growth with seasonal changes and compete effectively with neighbors for essential resources. Light signals are amongst the most important environmental cues regulating plant

development (Keara A. *etal*, 2003) . In addition to light quantity, plants monitor the quality, periodicity and direction of light and use the information to modulate multiple physiological responses, from seed germination and seedling establishment through to mature plant architecture and the onset of reproductive development (reviewed in Quail, 2002.)

Plants need to respond to light originating from different directions, with varying frequencies, qualities, and quantities. Thus, they can recognize wide bands of the light spectrum, ranging from UV-B through UV-A/blue and red (R) to far-red (FR) light, via several classes of photoreceptors, including phytochromes, cryptochromes, and phototropins. Phytochrome receptors are responsible for most of their light perception (Quail et al., 1995; Rockwell et al., 2006). The influence of CK/light crosstalk on dormancy breaking and initiation of germination has been described in many plant species (Miransari and Smith, 2014)

Light and phytohormones act as major external and internal factors respectively and they cross-talk with each other to control different aspects of plant growth in a coordinated manner (Kurepin et al. 2012). This cross-talk plays a crucial role in cotyledon development, seedling etiolation, hypocotyl elongation, root development, etc., throughout the plant's life (Nakazawa et al. 2001). However, the mechanisms behind this cross-talk have not been studied in depth and remain obscure. Classic experiments using maize coleoptiles have demonstrated that a unilateral blue-light stimulus causes auxin redistribution towards the shaded side of the illuminated organ, resulting in a differential growth response termed phototropic curvature (Briggs and Huala, 1999)

Research into the light dependence of ethylene biosynthesis has uncovered many important regulatory mechanisms. R light down regulates ethylene production in etiolated pea, rice, garden balsam, wheat, and bean seedlings, and in some cases, this negative effect of R light can be reversed by FR light (Steed et al., 2004).

2.1.8 Temperature signaling cross talk

Plants are sessile organisms that have to readily alter their development and growth responses to survive an ever-changing environment. This involves the correct amalgamation of multiple external signals including temperature and light, in all facets of development, from germination to flowering. Temperature is an environmental factor that has a considerable influence throughout the plant's developmental program. It plays a major role in controlling the degree of seed dormancy (Koornneef et al., 2002).

As sessile organisms, plants have evolved great plasticity to adapt to their surrounding environment (Achard P *et al*, 2008). Temperature signals regulate the timing of multiple developmental processes and have dramatic effects on plant architecture and biomass. Temperature regulates growth and development throughout the lifecycle of plants (Lorrain S *et al*, 2008). Many of the temperature-controlled responses are mediated via the manipulation of endogenous plant hormone levels and/or signal transduction. For example, gibberellic acid (GA) and abscisic acid (ABA) levels have been shown to be important factors in the regulation of seed dormancy (Koornneef et al., 2002). Both auxin and GA have been shown to have central roles in

temperature-controlled elongation responses. Auxin levels increase as ambient temperature rises, therefore, auxin-mediated effects on elongation growth are highly temperature-dependent (Gray et al., 1998). In many species, a prolonged period of cold (stratification) is required to promote germination through stimulation of GA biosynthesis. Conversely, high temperature treatment of seeds can inhibit germination, through induction of Abscisic Acid (ABA). The timing of reproductive development is also temperature sensitive in many species. In winter annuals, a prolonged period of cold (Vernalisation) is required to promote flowering the following spring (Dhaval Patel and Keara A, 2009). Growth of Arabidopsis at low temperatures results in a dwarfed and compact rosette habit, with leaves displaying increased thickness (Atkin OK, 2006). A graded increase in stem elongation, leaf area and plant biomass is observed with increasing temperature. In natural environments, it is likely that the difference between day and night temperatures has an important influence on plant architecture (Penfield S, 2006). The regulation of plant development by alternating thermocycles (thermoperiodism) is commonly exploited by the horticultural industry to modulate plant stature. Greater elongation of stems and leaves is generally observed when daytime temperatures exceed night temperature (positive DIF), whereas the opposite effect results with a converse regime (Myster J, Moe R, 1995). Growth at low temperatures (cold acclimation) enables plants to initiate signaling cascades and metabolic alterations, which enhance tolerance to freezing temperatures (Chinnusamy et al. 2003)

Summary

It is apparent that the signaling interactions among multiple phytohormones are rather common in controlling various growth and developmental processes. Plant growth and development involves the integration of many environmental and endogenous signals that, together with the intrinsic genetic program, determine plant form. Fundamental to this process are several growth regulators collectively called the plant hormones or phytohormones. This group includes auxin, cytokinin, the gibberellins (GAs), abscisic acid (ABA), ethylene, the brassinosteroids (BRs), and jasmonic acid (JA), each of which acts at low concentrations to regulate many aspects of plant growth and development.

Virtually every aspect of plant growth and development is under hormonal control to some degree. A single hormone can regulate an amazingly diverse array of cellular and developmental processes, while at the same time multiple hormones often influence a single process. Cross-talk" in hormone signaling reflects an organism's ability to integrate different inputs and respond appropriately, a crucial function at the heart of signaling network operation. Plant hormone involved in a variety of physiological aspects and plant stress responses. This review summarizes what is known about phytohormone cross talk signaling in the control of development and growth and provides an overview of emerging knowledge about connections between phytohormone, light and temperature.

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