MINIREVIEW

Auxin: a regulator of cold stress response

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The growth hormone auxin regulates essentially all aspects of plant developmental processes under optimum condition. However, as a sessile organism, plants encounter both optimal and non-optimal conditions during their life cycle. Various biotic and abiotic stresses affect the growth and development of plants. Although several phytohormones, such as salicylic acid, jasmonate and ethylene, have been shown to play central roles in regulating the plant development under biotic stresses, the knowledge of the role of hormones, particularly auxin, in abiotic stresses is limiting. Among the abiotic stresses, cold stress is one of the major stress in limiting the plant development and crop productivity. This review focuses on the role of auxin in developmental regulation of plants under cold stress. The emerging trend from the recent experiments suggest that cold stress induced change in the plant growth and development is tightly linked to the intracellular auxin gradient, which is regulated by the polar deployment and intracellular trafficking of auxin carriers.

Introduction

Growth and development of plants are regulated by both endogenous and exogenous factors. As endogenous factors, hormones play an indispensable role in regulating the developmental processes. Hormonal regulation of development is a complex process with interactions of 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 influences various developmental stages (Swarup et al. 2002, Chandler 2009, Depudyt and Hardtke 2011).

As a sessile organism, plant encounters various biotic and abiotic stresses during their life cycle. To survive under such non-optimal conditions, plants have evolved intricate mechanisms by which it perceives the external signals and responds accordingly. The abiotic stresses affect the worldwide crop production, which costs hundreds of millions of dollar every year (Mahajan and Tuteja 2005). Among the abiotic stresses, low temperature stress is a major stress in limiting the crop productivity. In 2009, chilling temperature alone resulted in crop damage equivalent to 158 billion yen in Japan (http://www.maff.go.jp/j/tokei/sokuhou/higai09_78910/index.html). In addition, early and late frosts also damage the vegetable and fruit productions. Unlike biotic stress, where the phytohormones salicylic acid, jasmonate, and ethylene have been shown to play central roles (Fujita et al. 2006), the role of hormones in abiotic stress is less clear. The only hormone that has a potential link to abiotic stress to date is abscisic acid (ABA). Interestingly, the role of ABA in cold stress remains unclear, as it has been shown that the low-temperature-regulated gene expression occurs relatively independent of ABA (Thomashow 1999, Xiong et al. 2002, Shinozaki and Yamaguchi Shinozaki 2006). Taken together, it is apparent that our

Abbreviations – ABA, abscisic acid; BR, brassinolide; *CBF*, C-repeat binding factor; GA, gibberellin; *gps*, gravity persistent signal; IAA, indole-3-acetic acid; *ICE1*, inducer of CBF expression 1; JA, jasmonic acid; PP2A, protein phosphatase 2A.

current understanding of roles of hormones in facilitating the plant growth and development under various abiotic stresses, including cold temperature, is limiting. This review focuses on cold stress and the plant hormone auxin and highlights the recent progress in this area.

Auxin transport, auxin gradient and plant development

The growth plasticity plays a major role in adaptation of plants to environmental changes. Numerous studies link the plant hormone auxin both at cellular and molecular levels to regulate the developmental plasticity, which powers the plant to adapt to continuous environmental changes. At optimum growth condition, a regulated and differential intracellular distribution of auxin aids many adaptation processes that include embryo patterning, organogenesis, meristem patterning and tropisms (Vieten et al. 2007). 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). This transport is directional because of the polar deployment of the efflux carriers at the membrane and controls the distribution of auxin within the tissues. Proteins belong to AUX/LAX and PIN families act as major regulators of cellular auxin transport by facilitating the influx and efflux, respectively. In addition, P-glycoproteins of the ABCB transporter family (ABCB/PGP) also mediate auxin efflux in both plants and heterologous systems (for review, see Peer et al. 2011). 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. 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).

In general, the patterning or formation of any organ starts with the accumulation of auxin followed by its redistribution to form a cellular or tissue-specific auxin gradient, which directs major developmental decisions, such as specification of the apical and basal poles and establishment of root and cotyledon (Friml 2003). Auxin gradient has also been shown to regulate organogenesis of leaves, flowers, floral organs, lateral roots and tropisms (Benkova et al. 2003, Muday and Rahman 2008). Formation of auxin gradient largely relies on the intracellular targeting of PIN proteins, which is a highly dynamic process with continuous cycling of the PINs between the cell surface and intracellular compartment (Geldner et al. 2001). Recent evidence suggests that constitutive cycling of PIN is mediated through clathrin-dependent endocytosis (Dhonukshe et al. 2007) and ARF-GEF-dependent exocytosis (Geldner et al. 2001). In addition, the phosphorylation status, which is regulated by the counterbalancing activities of PINOID kinase and protein phosphatase 2A (PP2A), also regulates PIN polarity and hence the flow of auxin (Michniewicz et al. 2007, Sukumar et al. 2009, Rahman et al. 2010).

Hormonal crosstalk: auxin at center

The growth and development of plant is regulated by a complex web of hormonal interactions. Interestingly, auxin has been found to be a common factor in majority of these interactions. 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 (for review, see Muday et al. 2012). Gibberellin (GA) and auxin have been shown to coordinately regulate pea stem elongation and parthenocarpy (for review, see 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 both root and 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) and embryonic axis formation (Belin et al. 2009).

Although some of these interactions are regulated at biosynthesis level such as auxin–ethylene (for review,

see Muday et al. 2012) or auxin–GA interactions (for review, see Chandler 2009) or at signaling level such as auxin–BR (Hardtke et al. 2007) or auxin–cytokinin (Moubayidin et al. 2009) interactions, the process that has been shown to be intrinsically involved in all the existing hormonal crosstalk is auxin transport. For instance, 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). Cytokinin modulates the cellular auxin gradient in root by regulating the expression of PIN1, PIN2 and PIN3 negatively but PIN7 positively (Ruzicka et al. 2009). In hypocotyl explants and cultured tobacco cells, cytokinin negatively regulates auxin efflux (Pernisova et al. 2009). The polar transport of auxin is also regulated by GA. In populous, GA stimulates the auxin transport and also induces the expression of PIN9, which has been linked to the lateral root development (Bjorklund et al. 2007, Gou et al. 2010). In *Arabidopsis*, GA deficiency has been shown to reduce the expression of PIN1 and PIN2 and promote the targeting of PIN2 proteins for vacuolar degradation, which affects the cotyledon differentiation and root gravitropism (Willige et al. 2011). The PIN expressions were found to be altered in BR synthesis/signaling mutants. In shoot, PIN1, PIN3 and PIN7 expressions are reduced in *dim1*, *det2* and *bri1* mutants, while in root, PIN2, PIN3 and PIN4 expression is compromised in *dim1* and *det2* mutants (Li et al. 2005). PIN2 localization in root was also found to be modulated by exogenous BR (Li et al. 2005). JA has been shown to alter the polar auxin transport by affecting the expression of auxin efflux carriers at both transcriptional and translational levels, and a recent report claimed that methyl JA affects the PIN2 subcellular distribution (Sun et al. 2009, Sun et al. 2011). Both *aux1* and *pin2* mutants are insensitive to ABA-dependent repression of embryonic axis (hypocotyl and radicle) elongation (Belin et al. 2009), and PIN1 expression in root has been shown to be altered in abscisic acid insensitive4 (*abi4*) mutant, suggesting that ABA also modulates auxin transport (Shkolnik-Inbar and Bar-Zvi 2010) Collectively, these results indicate that intracellular auxin transport,
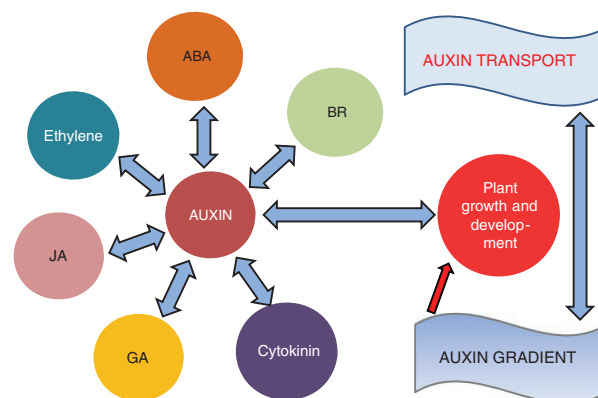
Fig. 1. Hormonal crosstalk regulating the plant growth and development, auxin at center. Various hormones interact with auxin in regulating the growth and development of plants at optimum condition. One of the common targets in these crosstalks is auxin transport, which alters the intracellular auxin gradient. This leads to the hypothesis that intracellular auxin gradient plays a central role in regulating the hormonal crosstalk and plant growth and development.

and hence the auxin gradient, plays a major role in controlling the auxin and other hormonal crosstalks that regulate the plant growth and development (Fig. 1). The intrinsic nature of auxin gradient in regulating the hormonal crosstalk and plant development at optimum temperature suggests that it may play a central role in regulating the plant growth under cold stress.

Cold stress response

Cold stress response in plants involves perception and relaying of the signal through a transcriptional cascade composed of different transduction components resulting in altered transcription of several genes. Although debatable, the plasma membrane has been suggested to be the primary site of cold perception as membrane composition changes both qualitatively and quantitatively in response to cold. Cold stress decreases the membrane fluidity as a result of changes in the fatty acid unsaturation and lipid–protein composition at cell membrane (Wang et al. 2006). Rigidification of membrane either by mutation or by exogenous application of membrane rigidifier results in inducing the cold-inducible genes even at room temperature (Orvar et al. 2000, Sangwan et al. 2002, Inaba et al. 2003). Hence, it is thought that membrane rigidification may play an important role in cold perception. Several membrane-located proteins have been suggested to be putative sensors for cold response. Experimental evidence suggests that calcium permeable channels, histidine kinase, receptor kinases, phospholipases and photosynthetic apparatus play a major role in relaying the cold signal

to downstream. Current model predicts that the cold stress signal is transduced to downstream signaling components through a series of phosphorylation cascade counterbalanced by PP2A and MAP kinase and regulated by cytosolic calcium (for review, see Solanke and Sharma 2008). Several transcription factors have been identified as the transcriptional regulators of cold-stress-induced genes. *ICE1* (inducer of CBF expression 1), a MYC-like transcription factor, which is activated by cold stress, has been placed at the beginning of transcriptional cascade (Xiong et al. 2002, Zhu et al. 2007). Recent evidence suggests that HOS1 (high expression of osmotically responsive genes), a ring type ubiquitin E3 ligase negatively regulates the function of ICE1 at low temperature by ubiquitin-mediated degradation (Dong et al. 2006a). On the other hand, Small Ubiquitin-related Modifier (SUMO) E3 ligase, SIZ1 stabilizes ICE1 at low temperature by repressing its polyubiquitination (Miura et al. 2007). Another R2R3-type MYB transcription factor, AtMYB15, was also found to physically interact with ICE1 (Agarwal et al. 2006). Taken together, these results suggest that phosphorylation and SIZ1-mediated SUMO conjugation and deconjugation of ICE1 are the key processes that activate ICE1 to bind its target genes. Active *ICE1* binds to *MYC cis*-elements in the *CBF* (C-repeat binding factor) promoter to induce the expression of target genes (Chinnusamy et al. 2003). The induction of the *CBF* genes at low temperature and the enhanced freezing tolerance of the transgenics overexpressing the CBFs suggest that this pathway (Fig. 2) plays a central role in regulating the cold stress response (Vogel et al. 2005). Although in other abiotic stresses hormones play an important role in transducing the stress signal to downstream (Fujita et al. 2006), in case of cold stress, the roles of hormones remain a mystery (Fig. 2).

Auxin and cold stress

Although auxin plays an essential role in regulating virtually all aspect of growth and development of plants, knowledge about its role under cold stress is limiting. The work that potentially link auxin to cold stress demonstrate that the inflorescence gravitropism of *Arabidopsis*, which is regulated by auxin, is inhibited by cold stress (Fukaki et al. 1996, Wyatt et al. 2002). Interestingly, the observed inhibition of inflorescence gravitropism at 4°C was transient, as both the gravity response and the rootward auxin transport, which were abolished at 4°C, returned to wild-type level when the plants were returned to room temperature (Fukaki et al. 1996, Wyatt et al. 2002, Nadella et al. 2006). These results suggest that during cold stress plant still retains its
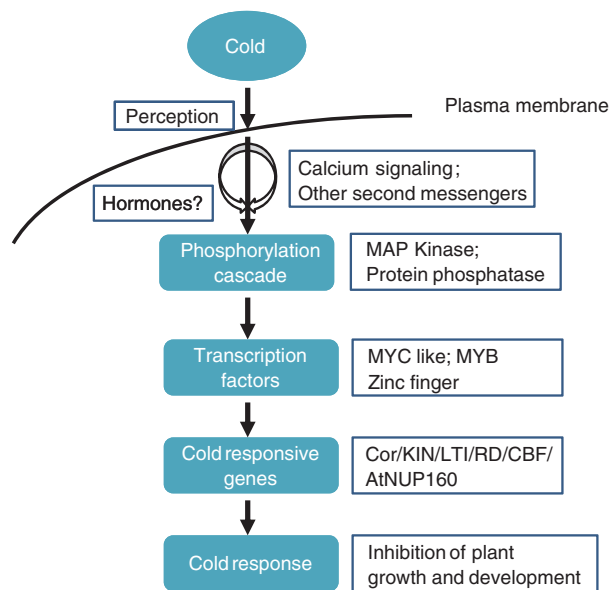

Fig. 2. Signal transduction pathway for cold stress in *Arabidopsis*.

capacity to perceive the gravity signal and indicate that cold stress affects the response process that is unlinked to perception. This idea was substantiated by isolation of gravity persistent signal (*gps*) mutants, which exhibit altered gravity response at room temperature after cold stress without showing any abnormality in amyloplast sedimentation, the process required for the first step of gravity perception (Sack 1991, Wyatt et al. 2002). Further analyses of *gps* mutants revealed that these mutants fail to establish a proper auxin gradient in the inflorescence after gravistimulation and also show altered polar and lateral auxin transport (Nadella et al. 2006). In an earlier report, Morris (1979) showed that temperature affects the velocity of exogenous auxin transport in a number of species. Collectively, these results suggest a potential link of auxin response in regulating the growth and development of plant under cold stress.

To understand the molecular and cellular events integrating the auxin response in cold stress, Shibasaki et al. (2009) performed a series of elegant experiments using *Arabidopsis* root. The response of auxin mutants to cold-stress-induced inhibition of root growth and gravity response, expression analysis of the auxin responsive marker *IAA2-GUS* and the direct auxin transport assay confirmed that cold stress primarily targets intracellular auxin transport (Shibasaki et al. 2009; Fig. 3). Most significantly, this study demonstrated that cold stress selectively inhibits the intracellular trafficking of a subset of proteins that include auxin efflux carriers. Intracellular-cycling-mediated asymmetric redistribution

of PIN3 facilitates the plants response to gravity (Friml et al. 2002, Harrison and Masson 2008). Cold stress blocks the asymmetric redistribution and intracellular cycling of PIN3 (Shibasaki et al. 2009). For shootward transport of auxin, recent molecular and cellular findings suggest that the polar deployment of PIN2 and the constitutive cycling of this protein from membrane to endosome are required for its functionality (Paciorek et al. 2005, Sukumar et al. 2009). Although cold stress does not alter the polar targeting of PIN2, it inhibits the intracellular cycling (Fig. 4). Collectively, these results suggest that the reduced intracellular cycling affects the PINs functionality resulting in reduced shootward transport of auxin and diminishes the root's capability to form an auxin gradient (Shibasaki et al. 2009). The idea that cold-stress-mediated inhibition of intracellular protein trafficking is selective was substantiated by analyzing the response of various trafficking pathways under cold stress. The endosomal trafficking, which was monitored by GFP-ARA7 (a homolog of Rab5 GTPase, Ueda et al. 2004), responded like PIN2; a considerable inhibition of movement was observed, while only a slight inhibition in golgi movement was observed under cold stress as judged by a widely used golgi marker, N-acetylglucosaminyl transferase fused to GFP (NAG-GFP). Interestingly, trafficking of a membrane protein, low-temperature-induced protein 6b (LTI6b, Kurup et al. 2005), which is induced by cold stress and shows a similar trafficking property like PINs, was not affected by cold stress (Fig. 4). Monitoring the general endocytosis under cold stress by using the general endocytic tracer FM 4-64 revealed that cold stress does not completely shut down all protein trafficking pathways (Shibasaki et al. 2009). In the same study, the authors also investigated the effect of change in membrane structure on PIN trafficking and auxin response. One of the earliest events of cold stress on cells is a change in fluidity of cellular membranes, leading to increase the membrane rigidity (Levitt 1980). By using the widely accepted artificial membrane rigidifier di-methyl sulfoxide (DMSO; Lyman et al. 1976, Orvar et al. 2000), the authors showed neither the root gravity response nor the trafficking of PIN2 is appreciably affected by membrane rigidification (Shibasaki et al. 2009). Collectively, these results confirm that immobilization of PINs during cold stress is not because of a global slowdown of trafficking or a change in the membrane structure but instead represents a selective process to regulate the activity of specific proteins, which provides a mechanistic basis to explain the role of auxin to regulate the plant growth and development under cold temperature stress.
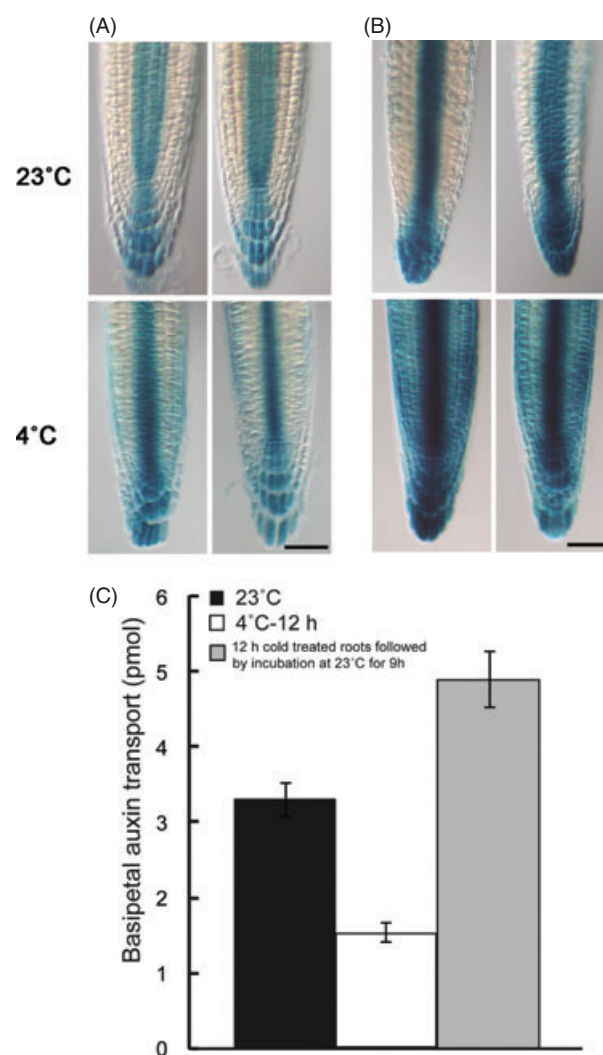
Fig. 3. Cold stress inhibits shootward auxin transport and alters the intracellular auxin gradient in *Arabidopsis* root. Intracellular auxin gradient under cold stress analyzed in the auxin responsive marker *IAA2-GUS*. (A) Control roots (top panel) and cold stressed roots (bottom panel); (B) roots in the presence of exogenous auxin. Seedlings were treated with 1 µM IAA for 30 min, control roots (top panel), and cold-treated roots (bottom panel). Bars = 50 µm (C) Effect of cold stress on shootward auxin transport. Reproduced from Shibasaki et al. (2009) with permission from the American Society of Plant Biologists.

More link to auxin and cold stress

Although the findings described above clearly demonstrate the importance of auxin in cold-stress-mediated plant growth and development, the question needs to be explored whether the currently known components of the cold signaling pathway are linked to auxin. Interestingly, the answer to this question is largely positive. SIZ1, a central regulatory component of cold signaling pathway, which stabilizes ICE1 at low
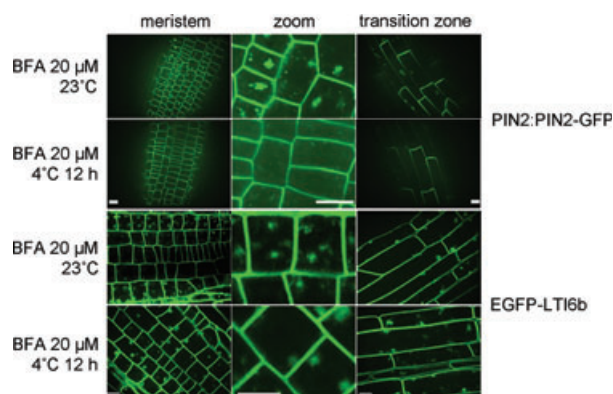
Fig. 4. Cold-stress-induced inhibition of protein trafficking is selective. Cold stress inhibits the intracellular dynamic cycling of PIN2 (upper rows) but not of LTI6b (lower rows). Bars = 10 and 50 μm in zoomed images. Reproduced from Shibasaki et al. (2009) with permission from the American Society of Plant Biologists.

temperature by repressing its polyubiquitination (Miura et al. 2007), has been shown to negatively regulate phosphate-starvation-induced root architecture remodeling through the control of auxin patterning (Miura et al. 2011). Another downstream component of cold signaling pathway is AtNUP160, a homolog of human nucleoporin NUP160, which plays a critical role for the nucleocytoplasmic transport of mRNAs under cold stress (Dong et al. 2006b). This AtNUP160/SAR1 has also been shown to play an important role in auxin signaling (Parry et al. 2006).

Concluding remarks

The current results link intracellular auxin response, which is regulated by the local auxin gradient, to developmental regulation of plant growth under cold stress. Interestingly, intracellular trafficking pathways, which are emerging as central regulators of PM protein homeostasis, controlling multiple signaling pathways and mediating interaction between multiple hormones and growth and development in both animals and plants, also found to be involved in regulating the auxin response under cold stress. Although these findings bring a new insight in our understanding how the cold stress and plant hormone auxin are integrated in regulating the plant growth and development, there are still many unanswered questions. Which protein trafficking pathway plays the central role in regulating the cold-stress-mediated inhibition of plant growth? How the change in the auxin response affects the other hormonal response under cold stress? Which components link the hormonal response to downstream signaling factors? Do the protein trafficking pathways globally regulate the plant stress response? Addressing these issues in future research will facilitate our understanding of stress response pathways and help in engineering crops tolerant to various abiotic stresses.

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