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COLD TOLERANCE IN PLANTS: A SIMPLE PHENOMENON WITH COMPLEX SIGNALING

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ABSTRACT

Plants face different abiotic stresses that reduce crop production worldwide. Cold stress is the main abiotic stress that reduce plant yield in hilly areas. Cold resistance in plants is considered to be an interesting phenomenon with complex signaling pathways. Tolerance to cold in plants is acquired by exposing them to a low non freezing temperature and involves extensive changes at molecular level. Understanding the molecular mechanism behind the cold resistance in plants can help us to develop more and more cold tolerant plants. This review discusses different molecular changes observed during development of cold tolerance in plants.

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INTRODUCTION

Plants withstand diverse range of cold and freezing temperatures (Sakai, 1987). Some plants of temperate regions are even able to survive in harsh cold conditions ranging from -5°C to -30°C. In most of the temperate plants, cold tolerance can be induced by exposing them to cold (non freezing) temperatures, a process called "cold acclimation" (LEVITT, 1980) and involves extensive beneficial molecular changes (SHINOZAKI, 1996) (Thomashow, 1998) (Gilmour *et al.*, 2000) (Thomashow, 2010) (Pearce S, 2013). Cold tolerance should not be confused with the cold acclimation, as former involves the ability to tolerate chilling temperatures (0–15°C) without injury or damage (C., 1995), while as later involves increased tolerance to freezing stress (C.L., 1990) (Thomashow, 1999). Understanding the molecular mechanism behind the increase in freezing tolerance associated with cold acclimation is of great scientific interest and has potential practical applications in agronomic plants.

Many approaches are presently in use to determine genes associated with the freezing tolerance, characterize genes activated during the process of cold acclimation and to study transcriptome. But how cold acclimation response is activated and what type molecular changes are associated during such process is of prime importance for investigators. It should be noted here that during cold acclimation, various physiological and molecular changes like transcriptional activation and repression of different genes has been reported (Thomashow, 1999). Such reprogramming at genomic level, results in activation of cytoprotective protein and other protective metabolites. Understanding such molecular changes is of great importance as traditional plant breeding approaches were not so successful in enhancing freezing tolerance (SARHAN, 1998).

Cold tolerance and molecular changes

An optimum temperature is needed for proper growth and development of a plant and this temperature vary for every species.

It should be further noted that the temperature conditions, which are optimum for one plant may pose stress for the other. Plants native to warm conditions shows damage upon exposure to cold condition (D.V., 1990). Appearance of cold associated injury symptoms depends mainly upon the sensitivity of a plant toward cold stress. Depending upon the intensity and duration of the cold stress, a wide spectrum of cellular components are affected. Cell membranes are considered to be the primary targets of cold injury in plants (LEVITT, 1980) (STEPONKUS, 1984). It was earlier proposed that cold acclimation might activate specific genes (J, 1970) and it was later on found that indeed there are changes in mRNA population (Guy *et al*., 1985). Cold acclimation has been associated with the induction of novel mRNA molecules and this provide basis for isolation of the corresponding cDNA molecules by differential screening and more recently by subtractive cloning and differential display. Till date various genes or corresponding cDNAs have been described in different plants including tomato (Schaffer M A, 1988), Arabidopsis (Hajela *et al*., 1990) (Nordin *et al*., 1991) (Nordin *et al*., 1993) (Gilmour *et al*., 1992) (Welin B V, 1994) (WeHn B V, 1995) (Jarillo *et al*., 1994), bromegrass (Lee S P, 1993), alfalfa (Monroy *et al*., 1993) (Castonguay *et al*., 1994), potato (van Berkel J. Salamini F, 1994) (Zhu, 1993) (Baudo MM, 1996), rice (Aguan *et al*., 1993), rye (Zhang L, 1993)), wheat (Holappa, 1995) (Chauvin *et al*., 1993) (Houde *et al*., 1992), spinach (Neven *et al*., 1993) (Anderson J V, 1994), barley (Dunn *et al*., 1991) (Goddard, 1993) and rapeseed (Saez-Vasquez, 1993) (Orr, 1992) (Orr *et al*., 1995). Cold acclimation process not only involves reprogramming of gene expression, but also various modifications in the metabolism (Chinnusamy, 2010.) like production of antioxidants, abscisic acid (ABA) and compatible osmolytes (soluble sugars and proline) (Kishitani, 1994.) (Uemura and Steponkus, 1994) (Murelli, 1995) (Dörffling, 1997) (Tao *et al*., 1998). Cold treatment increases membrane fluidity and thus helps protects cells against cold stress by maintaining cellular shape (TJ., 2007). There is increase in membrane rigidity during cold conditions; this change prevents cellular collapsing during extracellular freezing via creating a negative pressure in the cells and is an important response for cold tolerance (Rajashekar and Lafta, 1996) (Heidarvand L, 2010.) (Takahashi *et al*., 2013). It has been reported that during cold acclimation in Arabidopsis, there is an increase in clathrins and dynamin-related proteins in the microdomain during cold acclimation (Minami *et al*., 2009).

Furthermore, many different cytoprotective proteins like aquaporins, P-type ATPases and tubulins accumulate during cold acclimation (Minami *et al*., 2009) (Takahashi *et al*., 2013). During cold acclimation, large scale changes occur in transcriptome of a cell that ultimately produce a diverse array of cytoprotective proteins to avoid freezing injury (Kocsy *et al*., 2010) (Winfield *et al*., 2010). In Arabidopsis, transcriptome profiling has identified around 8000 cold response genes. Among them around 300 genes were affected by cold, of which 218 showed increased transcription and transcription of 88 genes were decreased within seven days of cold treatment (Fowler, 2002). To improve cold tolerance, majority of experiments have been carried with the Arabidopsis plant (Gery, 2011). In 2012, it was reported that Brachypodium distachyon can be used as an important model to unveil the molecular mechanism associated with the cold response (Li, 2012). Extensive studies have identified large number of genes associated with the cold tolerance, but such data raises a simple question, which genes are most central to increasing freezing tolerance? This has diverted the focus towards genes encoding a related family of cold-regulated (COR) proteins, which are induced massively during cold acclimation (Hajela *et al*., 1990) (Gilmour, 2004,). These COR genes have been classified as cold acclimation-specific (CAS), low temperature-induced (LTI), cold-induced (KIN) and responsive to drought (RD) genes (Kurkela and Franck, 1990) (Yamaguchi-shinozaki, 1992) (Monroy, 1993) (Nordin, 1993). The COR genes has been used to identify a family of Arabidopsis transcription factors known as either C-repeat binding factors (CBF) (CBF1, CBF2 and CBF3) or dehydration responsive element-binding factors (DREB) (DREB1B, DREB1C and DREB1A) (Stockinger, 1997) (Gilmour *et al*., 1998) (Liu *et al*., 1998). CBFs/DREBs are transcription factors (Tfs) that bind to promoter cis element CRT/DRE and activate expression of cold responsive genes (Thomashow, 1999). It has been found that the ectopic transgenic over expression of CBF1/DREB1B, CBF2/DREB1C or CBF3/DREB1A in Arabidopsis activates CBF/DREB target genes at warm temperatures (GILMOUR, 2004,) and therefore provides enhanced freezing, drought and salt tolerance (Jaglo-Ottosen *et al*., 1998) (Kasuga *et al*., 1999). When plants are exposed to low temperature conditions, CBF transcripts start accumulating within 15 minutes of exposure (Gilmour *et al*., 1998). Apart from COR genes, heat shock proteins (HSPs) expression are also induced under the effect of low temperature (Timperio *et al*., 2008). It has been further found that the bacterial cold shock proteins (CSPs) increases stress adaptation in multiple plant species by demonstrating enhanced stress tolerance in maize and rice. Expression of CspA and CspB enhances the growth of plants under the effect of a number of abiotic factors like cold, heat and water deficit in transgenic rice. Similarly expression of bacterial CSPs enhanced cold tolerance in transgenic Arabidopsis (Karlson D, 2003.) (Nakaminami *et al*., 2006) (Castiglioni *et al*., 2008). Transcript profiling studies have shown that the majority of cold sensitive genes are regulated by CBF, ZAT12 and RAV1 transcription factors. It should be noted here that the regulation mechanism of the majority of cold-induced COS genes and cold-repressed COS is unknown (Vogel *et al*., 2005). So understanding the regulatory mechanism of cold sensitive genes is of prime importance in understanding the cold acclimation fully.

Conclusion

The molecular changes associated with the plant cold tolerance are much more complex. But taking into account the essence of cold tolerance, it is need of the hour to understand the diverse cellular changes. New information regarding the cold-responsive pathway is continuously emerging and therefore making it a compulsory to gather the new information, so to simplify the complex changes associated with the plant adaptation to low temperature. It should be further noted that the research on low temperature changes in plants with respect to transcriptome, proteome and metabolome is expected to continue in the near future. In this review, we have gathered the earlier information to understand the complex network of molecular changes associated with the cold tolerance in plants.

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