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ARTICLE

Role of light in freezing tolerance of wheat

Tibor Janda*, Mátyás Pap, Gabriella Szalai

Agricultural Research Institute of the Hungarian Academy of Sciences, Martonvásár, Hungary

ABSTRACT During the frost hardening of wheat plants light intensity is a key factor in the development of frost tolerance, and several processes, including lipid metabolism, antioxidant activity, polyamine synthesis and salicylic acid signalling, may also contribute to light-enhanced freezing tolerance. The results suggest that there are at least two type of receptors, one cold- and one light-dependent, which induce signal transduction processes leading to freezing tolerance.

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KEY WORDS

acclimation processes
cold hardening
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Low temperature is one of the most important factors limiting the growth and distribution of plants. It is well known that even in frost-tolerant species a certain period of growth at low, but non-freezing temperature, known as frost hardening, is required for the development of frost hardiness. In wheat plants this cold acclimation includes changes in a wide range of physical and biochemical processes that allow functioning at low temperatures. It was shown in winter rye and wheat plants that frost hardening under low light conditions was much less effective than under normal light conditions (Gray et al. 1997). A certain level of freezing tolerance could also be induced by high light intensity without low temperature. The exact mechanisms of the contribution of light to the enhanced freezing tolerance of cereals during the hardening period are still poorly understood. The aim of the present work was to demonstrate the advantage of high light intensity during growth and its influence on the freezing tolerance of wheat plants with different levels of freezing tolerance, and to discover what physiological changes were responsible for this enhanced freezing tolerance.

Materials and Methods

Wheat plants (*Triticum aestivum* L.) were grown for 10 d in a growth chamber with a 16/8 h light/dark period, at 20/18°C (day/night) with 75% relative humidity and 250 µmol m^{-2} s^{-1} (control, normal light) photosynthetic photon flux density (PPFD). Low temperature hardening was carried out for 12 days at 5°C either under the light conditions of normal growth or at 20 µmol m^{-2} s^{-1} PPFD, or at high light intensity, achieved by lifting the plants closer to the light source of the growth chamber, where the PPFD was 500 µmol m^{-2} s^{-1}. To determine the ability of plants to tolerate freezing the pots were put in a frost chamber for 1 day at -12°C in the dark. Then the frozen seedlings were cut off at ground level and the regrowth of the plants was evaluated after 2 weeks.

*Corresponding author. E-mail: jandat@mail.mgki.hu

Polyamines were analysed as dansylated derivatives via HPLC using W2690 separation modules and a W474 scanning fluorescence detector (Waters, Milford, MA, USA) as described earlier (Német et al. 2002).

The analysis of glutathione S-transferase activity from the leaves was carried out as described earlier (Janda et al. 2003).

Results and Discussion

Earlier results showed that, as previously found in winter rye (Gray et al. 1997), the light intensity during the frost hardening of winter wheat plants is a key factor in the development of frost tolerance (Apostol et al. 2006; Janda et al. 2007a), and that several processes, including lipid metabolism and antioxidant activity, may contribute to enhanced freezing tolerance. Winter cereals need not only to survive, but also to grow and develop at low temperature to achieve maximum frost tolerance to survive the winter. Using thermoluminescence and measurements of P700 relaxation kinetics it has been shown that growth at low, hardening temperatures in the light increased the rate of cyclic photosynthetic electron transport, which may contribute to the higher frost tolerance observed after low temperature hardening in the light (Apostol et al. 2006). Cold hardening, under both normal and low light conditions, caused a significant increase in the 16:0 level, parallel with a decrease in the level of t16:1 in the phosphatidylglycerol lipid fraction. These changes occurred not only in plants hardened at low temperature, but also, to a lesser degree, in plants which were kept under high light irradiation. The 16:0 and 18:0 contents of phosphatidylethanolamine decreased with a concomitant increase in the 18:3 content, leading to a significant increase in the double bond index in plants hardened at low temperature under normal light conditions (Janda et al. 2007a).

Growth at low temperature may also cause excessive excitation of the electron transport systems, which may lead to an increase in the concentration of reactive oxygen species

(ROS). If the plants are not able to control the intracellular ROS level, the membrane lipids, proteins and nucleic acids may suffer damage, leading to the death of the cells. Low temperature hardening may induce the activity of certain antioxidant enzymes (Janda et al. 2003). However, this induction depends not only on the temperature, but also on the light. For example, the greatest induction of the enzymes glutathione reductase and ascorbate peroxidase occurred when the cold treatment was carried out in normal light, but elevated light intensity at normal, non-hardening temperature also increased the activity of these enzymes. The metabolism of the signal molecule salicylic acid, which may regulate several defence mechanisms (Horváth et al. 2007; Janda et al. 2007b), has also been shown to be involved in the light-mediated development of freezing tolerance in wheat (Janda et al. 2007a).

Besides the above-mentioned results, the exact mechanisms of the contribution of light during the hardening period to the enhanced freezing tolerance of cereals are still poorly understood. The use of wheat genotypes with different levels of frost tolerance showed that not only winter varieties, but also spring wheat genotypes can be frost hardened by growing under elevated light conditions; however, the effectiveness of hardening either at low temperature under low light conditions, or at non-hardening growth temperature with elevated light is more pronounced in plants with a higher level of freezing tolerance, indicating a correlation between the freezing tolerance acquired after hardening at low temperature and that induced by elevated light.

Polyamines are involved in defence mechanisms against various abiotic stress factors. Polyamine accumulation, especially that of putrescine and agmatine, has also been reported in wheat plants during both short- and long-term cold-hardening periods (Rácz et al., 1996). In order to obtain a better understanding of how frost hardening is regulated by light, the next aim of the present work was to demonstrate the role of light in the induction of polyamine synthesis in wheat plants with different levels of freezing tolerance under different temperature and light conditions. The present results showed that changes in the polyamine contents during low temperature hardening were dependent not only on genotype, but also to a marked extent on light. While the putrescine content showed a substantial increase in the winter wheat Mv Emese and a decrease in the spring wheat Nadro when the hardening was carried out under normal light conditions, it decreased at 5°C under low light conditions in both varieties. The content of the triamine spermidine, which is synthesized from putrescine, did not change at low temperature in the dark, but increased in the light. The most pronounced increase in the cadaverine content in the winter wheat Mv Emese also occurred, when it was cold hardened in the light. This polyamine was synthesized independently of the putrescine-spermidine-spermine pathway, and was thought to act as a free radical scavenger (Kuznetsov et al. 2007).

Glutathione is also involved in the detoxification of a wide variety of toxic compounds through its conjugation with them in a reaction catalysed by glutathione-S-transferases. In agreement with earlier results (Janda et al. 2003), low temperature hardening also induced the activity of the glutathione S-transferase enzyme in both the winter wheat Mv Emese and the spring wheat Nadro. In the present work this induction was shown to be more pronounced in the light than in the dark, and it was found that elevated light intensity at non-hardening temperature may also lead to increased activity.

The results suggest that there are at least two type of receptors, one cold- and one light-dependent, which induce signal transduction processes leading to freezing tolerance.

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