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Photosynthesis-dependent physiological and genetic crosstalk between cold acclimation and cold-induced resistance to fungal pathogens in triticale (*Triticosecale* Wittm.)

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ABSTRACT

The breeding for resistance against fungal pathogens in winter triticale (*Triticosecale* Wittm.) continues to be hindered by a complexity of the resistance mechanisms, strong interaction with environmental conditions, and dependence on the plant genotype. We showed, that temperature below 4 °C induced the plant genotype-dependent resistance against the fungal pathogen *Microdochium nivale*. The mechanism involved, at least, the adjustment of the reactions in the PSII proximity and photoprotection, followed by an improvement of the growth and development. The genotypes capable to develop the cold-induced resistance, showed a higher maximum quantum yield of PSII and a more efficient integration of the primary photochemistry of light reactions with the dark reactions. Moreover, induction of the photoprotective mechanism, involving at least the peroxidases scavenging hydrogen peroxide, was observed for such genotypes. Adjustment of the photosynthesis and stress acclimation has enabled fast plant growth and avoidance of the developmental stages sensitive to fungal infection. The same mechanisms allowed the quick regrow of plants during the post-disease period. In contrast, genotypes that were unable to develop resistance despite cold hardening had less flexible balancing of the photoprotection and photoinhibition processes. Traits related to: photosynthesis-dependent cold-acclimation and cold-induced resistance; biomass accumulation and growth; as well as protection system involving peroxidases; were integrated also at a genetic level. Analysing 95 lines of the mapping population SaKa3006 × Modus we determined region on chromosomes 5B and 7R shared within all tested traits. Moreover, similar expression pattern of a set of the genes related to PSII was determined with the meta-analysis of the multiple microarray experiments. Comparable results for peroxidases, involving APXs and GPXs and followed by PRXs, indicated a similar function during cold acclimation and defense responses. These data provide a new insight into the cross talk between cold acclimation and cold-induced resistance in triticale, indicating a key role of photosynthesis-related processes.

Introduction

Snow mold caused by *Microdochium nivale* (Fr.) Samuels and Hallett is the most widespread seedling disease of winter cereals. *M. nivale* is a fungal psychrophilic pathogen that is able to invade under the snow or during rainy, winter weather. The conditioning of the plant seedlings in low but positive temperature in the presence of light promotes genotype-dependent resistance to *M. nivale* infection (Gołębiowska and Wędzony, 2009; Szechyńska-Hebda et al., 2011). For cultivars able to develop resistance after cold treatment, increasing the duration of hardening from 0 to 98 days enhances plant survival and green biomass production almost linearly. In contrast, a period of 98 days still does not enable the susceptible cultivar to survive infection and regrowth of seedlings (Szechyńska-Hebda et al., 2013). It has been shown that

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M. nivale behaves as a biotroph in plants that are able to develop cold-induced resistance and as a necrotroph in tissues that are susceptible to infection (Szechyńska-Hebda et al., 2013). This fungal behavior has been linked to passive defense developed under light and cold temperatures in host leaves, and particularly to physical and chemical properties of the leaf surface as well as composition and structure of cell wall in the leaf interior (Szechyńska-Hebda et al., 2013).

The cold-induced resistance mechanism is dependent on the up-regulation of a wide range of stress-response genes (Gaudet et al., 2011). Recent research has identified genes encoding regulators of cold hardening and cold acclimation, e.g. COR (cold-responsive), LTI (low temperature-induced), RAB (responsive to abscisic acid), KIN (cold-induced) or ERD (early responsive to dehydration) proteins, antifreeze proteins, soluble carbohydrates contributing to an increase in cell osmotic potential, protein chaperones, and RNA chaperones (reviewed in detail by Ruelland et al., 2009). Moreover, it has been shown that cold acclimation of winter crops involves genotype-dependent changes in hormone composition, stress-related protective substances (proline, phenolics), and cellular redox status (Majláth et al., 2012). Although a large number of genetic and biochemical responses triggered by cold hardening can be universal and useful for a plant in its defense processes, the exact mechanisms involved in cold-induced resistance to pathogens still remains to be identified.

Some evidence indicates the key role of photosynthesis in the induction of plant resistance by cold. First, it is known that the acquisition of cold acclimation and resistance requires light (Ruelland et al., 2009), which is a driving force for photosynthesis. The hardening of cereals, such as rye or wheat, is much more effective under normal light conditions than under low light conditions (Janda et al., 2014). Light has a significant, genotype-dependent effect on the expression level of genes involved in the hardening process; but also genes that reflect overlapping between the signaling routes of abiotic stress tolerance and pathogen defense (Majláth et al., 2012). Among others, the regulation of photosynthesis-related genes, stress-related genes, and genes related to the N-metabolism was recognized as a necessary condition of the acclimation responses (Rapacz et al., 2008; Liu et al., 1998; Janda et al., 2014) and defense responses (Bilgin et al., 2010). Second, the excitation level of photosystems is a critical factor in both, abiotic stress acclimation and resistance induction (Huner et al., 1993; Szechyńska-Hebda et al., 2010; Karpiński and Szechyńska-Hebda, 2010). Light energy trapping by the antenna of PSII and PSI, use of this energy to drive charge separation within the reaction center cores, are both largely temperature-independent, but in contrast, low temperatures inhibit thylakoid electron transport by increasing membrane viscosity and restricting the diffusion of plastoquinone. Therefore, under cold conditions, an imbalance occurs within the amount of light energy absorbed by primary photochemical reactions in PSII and PSI, the transformation of this energy into NADP and ATP, and its utilization in metabolism (Ruelland et al., 2009). The excess excitation energy and reduction state of PS II has been shown to correlate with the induction of certain light-, cold- and defense-related genes (Szechyńska-Hebda et al., 2010; Karpiński and Szechyńska-Hebda, 2010; Janda et al., 2014). Third, photosynthesis-originated ROS and mechanisms of their scavenging determine the outcome of cold stress and pathogen-generated injuries. Excess excitation energy induced by the cold under light conditions in the light-harvesting chlorophyll antennae can favor the production of ROS, inactivation of PSII, chloroplast membrane damages and photoinhibition. On a time scale of minutes, plants can acclimate by diverting energy from PSII to PSI through state transitions or by dissipating excess energy as heat by non-photochemical quenching. On a longer time scale, photosynthetic acclimation may occur as a consequence of a reduction in PSII antenna size and an increase in the capacity for ROS scavenging (Huner et al., 1993; Ruelland et al., 2009). In particular, the expression of the genes encoding iron superoxide dismutase, glutathione-dependent peroxidases and ascorbate peroxidases was specifically regulated during the acquired acclimation to abiotic stress and acquired resistance to pathogens (Ruelland et al., 2009; Szechyńska-Hebda and Karpiński, 2013). Fourth, cold induces changes in the plant carbohydrate metabolism, an outcome of photosynthesis (Ruelland et al., 2009; Janda et al., 2014). Genotype-dependent acclimation involves modification of both protective (cytosolic) and structural (cell wall) carbohydrates, thus influences the level of plant's resistance or susceptibility (Majláth et al., 2012; Szechyńska-Hebda et al., 2013). Fifth, recent results showed that besides changes in PSII and alterations in (anti)oxidative status, several other mechanisms originated in chloroplasts, including salicylic acid metabolism may also contribute to the resistance induced by cold and/or light (Karpiński et al., 2013; Janda et al., 2014). Light is known to affect SA metabolism during cold hardening and it has also been shown that the overexpression of a salicylic acid (SA)-inducible Dof (DNA binding with one finger) transcription factor (OBP3) resulted in growth defects. The signaling sugar molecules are yet another potential regulator of Dof domain transcription factors (Kang and Singh, 2000; Janda et al., 2014). Thus, it can be assumed that role of SA and signaling sugar can be physiologically integrated and play a role in the control of nuclear genes and growth regulation induced by light and low temperatures.

Since a plant must adjust its photosynthetic activity during hardening in order to achieve appropriate acclimation and defense responses (Huner et al., 1993), in the present studies we tried to answer the following questions: (1) What photosynthesis-related mechanisms are common and required for both, plant acclimation to cold and resistance to fungal pathogen? (2) Can plants adjust their photosynthesis to enable fast plant growth and to avoid developmental stages that are sensitive to fungal infection? (3) How do changes in photosynthesis during cold hardening process contribute to resistance reactions and plant regrowth after infection? and (4) Is the peroxidases activity a part of the strategies that help to reduce oxidative stress during cold hardening and cold-induced resistance? With a set of 95 doubled haploid (DH) lines originating from a cross between ×*Triticosecale* Wittm. SaKa3006 and Modus, a comparable analysis of traits between hardened and unhardened plants was performed. As a result, we determined a tight correlation between the cold acclimation and cold-induced resistance on both the physiological level (growth and development, photosynthesis efficiency expressed as F_v/F_m and PI, peroxidases activity) and the genetic level (QTL analysis of physiological traits and metaanalysis of transcripts related to PSII and peroxidases).

Materials and methods

Plant material and growth conditions

A population of 95 DH lines originated from an intercultivar cross between two unrelated hexaploid winter triticales (*Triticosecale* Wittm.) was studied (Tyrka et al., 2011). The breeding line SaKa3006 (SaKa Pflanzenzucht GbR, Germany) was used as a female parent and the cultivar Modus (registered in Poland, released by Plant Breeding Strzelce Ltd.) was the pollen parent. The cultivars SaKa3006 and Modus were chosen as parents because of their different origin and different responses to cold-induced resistance to *Microdochium nivale*. Modus has been described as a cultivar able to develop partial resistance after cold treatment, and SaKa3006 as a cultivar susceptible to fungal infection despite plant hardening with cold. The seeds of the parent plants and lines of