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Changes in carbohydrates triggered by low temperature waterlogging modify photosynthetic acclimation to cold in *Festuca pratensis*

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ABSTRACT

Increased precipitation expected during autumn and winter at higher latitudes in the northern hemisphere may lead to low temperature short-term waterlogging. The temperature of waterlogging was shown to be an important factor controlling plant reaction to this stress. Photosynthetic apparatus response to water excess in the soil at low temperature was examined in *Festuca pratensis* genotypes with contrasting freezing tolerance. The study was aimed to test the hypothesis whether changes in leaf water-soluble carbohydrate concentration brought about alterations in Rubisco activity may affect the photoacclimation to cold under water excess in the soil. The study investigated the effects of waterlogging during cold acclimation process on a set of chlorophyll *a* fluorescence parameters, water-soluble carbohydrates, expression of Rubisco activase gene, and Rubisco activity. It was shown that carbohydrate status affected by Rubisco activity might be crucial for the activation of non-photochemical mechanism of photoacclimation to cold under waterlogging. Altered Rubisco activity was only partially attributed to the expression of Rubisco activase gene. Additionally, low carbohydrate concentration in the leaves of waterlogged plants was the condition preventing sugar repression of photosynthesis, including *Rca*A expression. This indicates that sugar de-repression of photosynthetic genes may be considered a component of photosynthetic acclimation to cold under waterlogging.

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1. Introduction

Short-term waterlogging often takes place in natural environment. Such conditions may occur even more frequently as increased precipitation is expected during autumn and winter at higher latitudes in the northern hemisphere (Stocker et al., 2013). A major result of water excess is an inadequate supply of oxygen to the submerged tissues (Armstrong and Drew, 2002). One of the effects of oxygen deficiency is an accelerated use of carbon reserves leading to an energy crisis (Drew, 1997). Flooding at low temperature is less detrimental than flooding at high temperature (Beard and Martin, 1970), as an increase in temperature is associated with greater enzyme activity and lower oxygen solubility. As the result, different mechanisms of acclimation may be activated when flooding occurs at different temperatures. Although extensive research has been performed concerning plant responses to water excess, relatively little is known about plant responses at low temperatures.

Exposure to low, non-freezing temperatures results in freezing tolerance increase in cold tolerant species. This phenomenon, termed cold acclimation (CA), is associated with changes at structural, physiological and biochemical level (Thomashow, 1999). Photosynthetic processes should also be adjusted to low temperature, as enzymatic reactions are more strongly inhibited than the photophysical and photochemical processes during photosynthesis (Ensminger et al., 2006). These photoinhibitory conditions triggered by low temperature induce an acclimation of the photosynthetic apparatus (Crosatti et al., 2013). To avoid cold-induced photoinhibition of photosynthesis, higher plants may activate photochemical or/and non-photochemical (NPQ) mechanisms within the photosynthetic apparatus. The photochemical mechanism depends on increasing energy utilization, while the NPQ mechanism relies on harmless dissipation of the excess of excitation energy in the form of heat (Huner et al., 1993). Both mechanisms may be activated at the same time and their intensity is genotype-dependent (Rapacz et al., 2004). Activation of NPQ

Abbreviations: ABS, absorption flux; CA, cold acclimation; CS, leaf cross-section; DI_0, dissipation flux; ET_0, electron transport flux; F_m', maximum fluorescence measured on a light-adapted sample; F_s, steady state fluorescence; F_v', fluorescence change between F_0' and F_m'; F_0', minimum fluorescence measured in a light-adapted sample; NPQ, non-photochemical quenching; PI, PSII performance index; q_P, photochemical quenching; RA, Rubisco activity; RC, reaction centre; TR_0, energy flux for trapping; WSC, water-soluble carbohydrates; Φ_{PSII}, quantum yield of electron transport at PSII.

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mechanism may contribute to better freezing tolerance under low temperature (Humphreys et al., 2007), but also under low temperature waterlogging (Jurczyk et al., 2015a). However, a stable increase in the freezing tolerance observed under low temperature waterlogging seems to be related rather to elevated carbohydrate concentration (Jurczyk et al., 2013).

Increased activity of many Calvin cycle enzymes, including Rubisco, was observed after CA (Hurry et al., 1994, 1995a,b). The increase in Rubisco activity after CA was higher in more freezing-tolerant plants (Huner et al., 1993; Hurry et al., 1995b) and was attributed to an increase in its specific activity rather than an accumulation of Rubisco protein. On the other hand, a drop in Rubisco activity was observed in waterlogged barley plants as a result of restricted synthesis of both Rubisco subunits (Yordanova and Popova, 2001; Yordanova et al., 2004). The catalytic competence of Rubisco is attained following its activation by Rubisco activase in an ATP-dependent reaction (Spreitzer and Salvucci, 2002; Portis 2003). Two isoforms of Rubisco activase were evidenced in *Festuca pratensis* as a result of alternative splicing of a single gene (Jurczyk et al., 2015b). In control plants, the shorter splicing variant was preferentially produced. The differences in isoform levels resulted from differences in their mRNA levels, indicating that transcriptional control of Rubisco activase gene may affect Rubisco activity. Furthermore, a decrease in a short Rubisco activase isoform was observed after prolonged CA in a low freezing tolerant *F. pratensis* genotype (Kosmala et al., 2009).

F. pratensis (Fp) is the most freezing tolerant species within *Lolium–Festuca* complex and can be considered a donor of freezing tolerance components to closely related *Lolium perenne* and *Lolium multiflorum* (Kosmala et al., 2006). Fp can be used as a model to identify the mechanisms involved in the CA and photosynthetic acclimation to cold under the waterlogging stress. The study was aimed to test the hypothesis whether changes in leaf water-soluble carbohydrate concentration brought about alterations in Rubisco activity may affect the photoacclimation to cold under water excess in the soil. Our second goal was to verify whether the changes in Rubisco activity under waterlogging at low temperature correspond to a transcriptional control of Rubisco activase gene.

2. Material and methods

2.1. Plant materials and stress treatment

The experiments were performed on four *F. pratensis* (Huds.) cv. Skra genotypes, named Fp1, Fp4, Fp6, and Fp20, selected from a population of 20 genotypes as previously described (Jurczyk et al., 2015a). Fp1 and Fp4 were shown to be highly freezing tolerant, while Fp6 and Fp20 were low freezing tolerant genotypes under the control conditions. Freezing tolerance of Fp4 decreased as a result of waterlogging after 3 weeks of CA, while in Fp1, Fp6 and Fp20 it was not affected (Jurczyk et al., 2015a). The germination of seeds and seedling growth took place under controlled conditions (20 °C, 12/12 h photoperiod, 200 μmol m^{-2} s^{-1} PAR administered by Agro HPS lamps, Philips), as described by Jurczyk et al. (2015a). When the plants were one year old, the individuals from each genotype were cloned into five parts two of which were exposed to waterlogging and two were controls (two clones per treatment per genotype). Both groups were cold acclimated for 21 days (4/2 °C, 12/12 h photoperiod, 200 μmol m^{-2} s^{-1} PAR administered by Agro HPS lamps, Philips, Brussels, Belgium). The waterlogged plants were flooded in tap water (pH 7.5, dGH = 273 mg/dm^3) by filling the pots up to ca. 2 cm above the soil line. The control plants were irrigated optimally. The fifth clone was maintained under the controlled environment (20 °C, 12/12 h photoperiod, 200 μmol m^{-2} s^{-1} PAR). When the plants were 15 months old, the fifth clone was divided into four clones (two for control and two for waterlogging), and the experiment was repeated.

2.2. Chlorophyll fluorescence

The measurements of leaf chlorophyll fluorescence were performed with Plant Efficiency Analyzer PEA and modulated fluorescence system FMS2 (Hansatech, Kings Lynn, UK) after 7, 14 and 21 days of CA in the control and waterlogged plants. The measurements were taken under CA conditions in the central part of the youngest mature leaves. Before measurements, the leaf fragments were put for 20 min into leaf clips for dark adaptation.

2.2.1. FMS2

A modulated fluorescence system FMS2 was used for chlorophyll *a* fluorescence measurements to estimate PSII photochemical efficiency. The source of a modulation beam (duration pulses 1.8 μs, 2.3 kHz) was an amber LED (594 nm, photon flux density 0.05 μmol m^{-2} s^{-1}). Actinic and pulse irradiations were administrated by a halogen lamp (20 W). The measurements were taken at actinic irradiance 500 μmol m^{-2} s^{-1}. Each leaf was illuminated for 5 min until stabilization of the fluorescence signal (F_s). Intensity of the saturating pulse (F_m') was about 5800 μmol m^{-2} s^{-1} and it lasted for 0.9 s. F_o' was measured when the actinic light was turned off after 3 s long far red pulse. Quantum yield of electron transport at PSII (Φ_{PSII}), photochemical quenching (q_P) and efficiency of energy capture by open PSII reaction centres (F_v'/F_m', where $F_v' = F_m' - F_o'$) were calculated according to Genty et al. (1989). The results are means of two experimental series (12 measurements per genotype per treatment).

2.2.2. PEA analyser

Polyphasic chlorophyll *a* fluorescence kinetics (Strasser et al., 1995) was determined for the excitation irradiance of 3000 μmol m^{-2} s^{-1}, 1 s pulse duration and fixed gain (×0.8). Handy PEA v.1.3 software (Hansatech, UK) was used for chlorophyll fluorescence parameter calculations, according to the theory of energy distribution in photosystem II and the equations of JIP test (Strasser and Tsimilli-Michael 2001; Strasser et al., 2005; Rapacz, 2007). Three groups of parameters were taken into account: (1) specific energy fluxes (per Q_A-reducing photosystem II reaction centre, RC and per excited cross section, CS), ABS/RC and ABS/CS (light energy absorption per RC and CS), ET_0/RC and ET_0/CS (electron transport flux), TR_0/RC and TR_0/CS (flux for energy trapping in PSII reaction centres), DI_0/RC and DI_0/CS (dissipated energy flux), (2) yields or flux ratios, TR_0/ABS (F_v/F_m, maximum quantum yield of primary photochemistry), ET_0/TR_0 (efficiency at $t = 0$ of moving an electron beyond Q_A^- into the electron transport chain), ET_0/ABS (probability that an absorbed photon will move an electron within the electron transport chain, at $t = 0$), and (3) PSII performance index, PI (summarizing three main functional steps in PSII, i.e. light energy absorption, excitation energy trapping and energy conversion to electron transport), and the minimum and maximum density of active reaction centres per leaf cross-section, RC/CS_0 and RC/CS_m. The results are means of two experimental series (20 measurements per genotype per treatment).

2.3. Analysis of Rca*A* transcript accumulation

Samples (ca. 0.04 g from the central part of the youngest mature leaves) were cut under sterile conditions from control and waterlogged Fp1, Fp4, Fp6 and Fp20 plants after 7, 14 and 21 days of CA. After collection, the samples were frozen in liquid nitrogen and stored at −80 °C. RNeasy Plant Mini Kit (Qiagen, Hilden, Germany) was used for RNA extraction. Purified RNA samples were incubated with gDNA Wipeout Buffer for genomic DNA elimination

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