Plant Physiology and Biochemistry 101 (2016) 68–75

Contents lists available at ScienceDirect

Plant Physiology and Biochemistry

journal homepage: www.elsevier.com/locate/plaphy

Research article

Salt acclimation processes in wheat

Tibor Janda [a,*], Éva Darko [a], Sami Shehata [b], Viktória Kovács [a], Magda Pál [a], Gabriella Szalai [a]

[a] Agricultural Institute, Centre for Agricultural Research, Hungarian Academy of Sciences, H-2462 Martonvásár, POB 19, Hungary
[b] National Research Centre, El Buhouth St., Dokki, Cairo, Egypt

A R T I C L E I N F O

Article history:
Received 7 January 2016
Received in revised form
28 January 2016
Accepted 29 January 2016
Available online 2 February 2016

Keywords:
Acclimation
Gene expression
Oxidative stress
Salinity
Triticum aestivum L.

A B S T R A C T

Young wheat plants (*Triticum aestivum* L. cv. Mv Béres) were exposed to 0 or 25 mM NaCl for 11 days (salt acclimation). Thereafter the plants were irrigated with 500 mM NaCl for 5 days (salt stress). Irrigating the plants with a low concentration of NaCl successfully led to a reduction in chlorotic symptoms and in the impairment of the photosynthetic processes when the plants were exposed to subsequent high-dose salt treatment. After exposure to a high concentration of NaCl there was no difference in leaf Na content between the salt-acclimated and non-acclimated plants, indicating that salt acclimation did not significantly modify Na transport to the shoots. While the polyamine level was lower in salt-treated plants than in the control, salt acclimation led to increased osmotic potential in the leaves. Similarly, the activities of certain antioxidant enzymes, namely glutathione reductase, catalase and ascorbate peroxidase, were significantly higher in salt-acclimated plants. The results also suggest that while SOS1, SOS2 or NHX2 do not play a decisive role in the salt acclimation processes in young wheat plants; another stress-related gene, *WALI6*, may contribute to the success of the salt acclimation processes. The present study suggested that the responses of wheat plants to acclimation with low level of salt and to treatment with high doses of salt may be fundamentally different.

© 2016 Elsevier Masson SAS. All rights reserved.

1. Introduction

High salinity is one of the most widespread abiotic stress factors in agriculture, causing problems in plant production both on naturally saline soils and on irrigated lands with unsuitable water management or exposure to high evaporation. Depending on the level of the stress and the stage of plant development, high salinity may induce various physiological malfunctions (Hossain et al., 2015; Kranner and Seal, 2013). Osmotic stress, as a primary reaction triggered by relatively moderate salinity levels, decreases soil water potential, reduces water uptake and may cause cell dehydration, stomatal closure and a decline in photosynthetic activity, leading to a limited growth rate. At high salinity ionic stress may also occur when ions are taken up by plants at an above-optimum concentration. Specific ionic stresses lead to a disruption of the integrity and selectivity of the root plasma membrane, the homeostasis of essential ions, and numerous metabolic activities.

Plants have developed several survival mechanisms to reduce the damaging effects of high salinity. These processes include the selection or exclusion of undesirable ions, the control of ion uptake by the roots and their transport into the leaves, the compartmentalization of ions at the cellular and whole-plant levels, the synthesis of compatible solutes, the adjustment of photosynthetic processes, alterations in membrane structure, the induction of antioxidant enzymes to reduce the level of oxidative stress, and the reprogramming of plant hormone synthesis (reviewed by Parida and Das, 2005). An important component of salt tolerance in plants is the minimising of Na^+ uptake by the roots. The salt-overly-sensitive (SOS) signal-transduction pathway is important for ion homeostasis and salt tolerance in plants. In this system a salt-induced transient increase in the Ca^{2+} level is sensed by the calcium-binding protein SOS3, which activates the serine/

Abbreviations: APX, ascorbate peroxidase; C_i, intracellular CO_2 concentration; E, transpiration; F_v, variable fluorescence at dark adapted state; F_m, maximum fluorescence at dark adapted state; G-POD, guaiacol peroxidase; GR, glutathione reductase; g_s, stomatal conductance; NPQ, non-photochemical quenching; Pn, net photosynthesis; PPFD, photosynthetic photon flux density; PSII, Photosystem II; ROS, reactive oxygen species; WUE, water use efficiency.

* Corresponding author.
E-mail addresses: janda.tibor@agrar.mta.hu (T. Janda), darko.eva@agrar.mta.hu (É. Darko), sami.shehata@gmail.com (S. Shehata), kovacs.viktoria@agrar.mta.hu (V. Kovács), pal.magda@agrar.mta.hu (M. Pál), szalai.gabriella@agrar.mta.hu (G. Szalai).

http://dx.doi.org/10.1016/j.plaphy.2016.01.025
0981-9428/© 2016 Elsevier Masson SAS. All rights reserved.

threonine protein kinase SOS2. The SOS2/SOS3 complex activates the plasma membrane Na^+/H^+ exchanger protein SOS1 (Hasegawa et al., 2000; Qiu et al., 2002). In Arabidopsis 8 isoforms of Na^+/H^+ antiporter genes (NHX homologues) have been described (Bassil and Blumwald, 2014). *AtNHX1* and *AtNHX2* are highly expressed in many tissues, while *AtNHX3* and *AtNHX4* are exclusively expressed in flowers and roots (Aharon et al., 2003; Yokoi et al., 2002). Recent results also suggested that NHX1 and NHX2 are vacuolar K^+/H^+ exchangers that control vacuolar pH and K+ homeostasis, they are essential for active K^+ uptake at the tonoplast, osmotic adjustment and turgor regulation, and that they play a unique role in stomatal function (Bassil et al., 2011; Barragan et al., 2012).

The exposure of plants to a moderate level of a stressor may induce protective mechanisms enabling the plants to tolerate a subsequent drastic stress factor (Janda et al., 2014). Pre-treatment of plants with a low concentration of NaCl has also been reported as an effective process to induce a higher level of salt tolerance. This phenomenon is usually referred to as salt acclimation or acquired salinity tolerance (Amzallag et al., 1990; Umezawa et al., 2000; Pandolfi et al., 2012).

Although a large body of data has been collected on the mechanisms of salt tolerance in various plants species, much less is known about the physiological and molecular background of salt acclimation processes, especially in monocot cereals. In the present work it was demonstrated that the treatment of young wheat plants with a low concentration of NaCl may increase their tolerance to a subsequent high-dose salt stress. Certain key mechanisms responsible for the improved salt tolerance induced by salt acclimation were also revealed by comparing the effects of acclimation with a low salt level and the responses of wheat plants to a high dose of salt.

2. Materials and methods

2.1. Plant material and growth conditions

Wheat plants (*Triticum aestivum* L. var. Mv Béres) were grown under controlled growth conditions in a Conviron PGR-15 plant growth chamber (Controlled Environments Ltd, Winnipeg, Canada) in the phytotron of the Agricultural Institute, Centre for Agricultural Research, Hungarian Academy of Sciences, Martonvásár at 22/20 °C day/night temperature, 75% relative humidity and approx. 320 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD), in 12 cm diameter pots filled with loamy soil and irrigated occasionally with tap water. After a week half the pots were irrigated with 25 mM NaCl solution dissolved in tap water for 11 days (salt acclimation). After the acclimation period, the plants were irrigated with 500 mM NaCl (salt stress).

For biochemical and physiological analyses the middle parts of the youngest fully expanded leaves were used. Samples were collected after 1 day of high salinity for polyamine, antioxidant enzyme, gene expression and after 5 days for pigment and Na content measurements and for the osmotic potential determinations. Gas exchange and chlorophyll fluorescence induction measurements were also carried out on intact leaves after 1 or 5 days after treatment with 500 mM NaCl, respectively.

2.2. Measurement of photosynthetic pigments

The chlorophyll (*a* and b) and carotenoid contents of the leaves were determined spectrophotometrically after extracting the leaf segments (100 mg per sample) in 80% acetone, according to the method of Lichtenthaler (1987).

2.3. Gas exchange measurements

Gas exchange analysis was performed on intact leaves with a Ciras 2 Portable Photosynthesis System (Amesbury, USA) using a narrow leaf area (2.5 cm^2) chamber. The measurements were performed 1 day after salt stress treatment. The parameters CO_2 assimilation rate (Pn), stomatal conductance (g_s), intracellular CO_2 concentration (C_i) and transpiration (E) were determined at the steady-state level of photosynthesis. The reference level of CO_2 was 380 μL L^{-1} and the light intensity was 250 μmol m^{-2} s^{-1}.

2.4. Fluorescence induction measurements

Chlorophyll *a* fluorescence quenching analysis was carried out using a pulse amplitude modulated fluorometer (Imaging-PAM M-Series fluorometer; Walz, Effeltrich, Germany) on detached leaves of wheat plants with or without salt stress (500 mM NaCl) for 5 days. The plants were previously dark-adapted for 20 min, after which the F_v/F_m parameter was determined using a 0.8 s saturation pulse (PPFD = 3000 μmol m^{-2} s^{-1}) provided by a LED-Array Illumination Unit IMAG-MAX/L ($\lambda = 450$ nm). Photosynthesis was then activated using 230 μmol m^{-2} s^{-1} actinic light intensity for 15 min and the quenching analysis was performed using a 30 s saturation pulse frequency. The quenching parameters were determined under steady state conditions according to the nomenclature described by Klughammer and Schreiber (2008).

2.5. Determination of Na content

The Na content in the leaves was determined from air-dried samples (approx. 0.5 g of each sample) using the inductively coupled plasma-atomic emission spectrometry method (ICP-AES, Jobin-Yvon Ultima 2 sequential instrument) after microwave Teflon bomb digestion with cc. HNO_3+HCl (Anton et al., 2012).

2.6. Osmotic potential measurements

The osmolarity of the leaf sap from control, salt-acclimated and salt-stressed leaves with and without acclimation was measured using a cryoscopic osmometer, Osmomat 3000 (Gonotech GmbH, Berlin, Germany) and the osmotic potential values (Ψ_π) were calculated as described by Bajji et al. (2001). Samples for analysis were collected after 5 days of salt stress.

2.7. Polyamine determination

Polyamine analysis was carried out from leaf segments as described by Németh et al. (2002). Two hundred milligrams of leaves were homogenized with 1 ml 0.2 M ice-cold perchloric acid and were allowed to stand for 20 min on ice. The extract was centrifuged at 10 000*g* for 20 min and the supernatant was used. The polyamines were analysed as dansylated derivatives via HPLC using a W2690 separation module and a W474 scanning fluorescence detector with excitation at 340 nm and emission at 515 nm (Waters, Milford, MA, USA). Conjugated and bound forms of PAs were measured after 1 + h of acid hydrolysis at 96 °C.

2.8. Measurements of antioxidant activities

For the analysis of antioxidant enzyme activity, 0.5 g tissue was homogenized in 2.5 ml ice-cold Tris–HCl buffer (0.5 M, pH 7.5) containing 3 mM $MgCl_2$ and 1 mM EDTA.

The glutathione reductase (GR; EC 1.6.4.2.) activity was determined at 412 nm according to Smith et al. (1988). The reaction mixture contained 75 mM Na-phosphate buffer (pH 7.5), 0.15 mM

Download English Version:

https://daneshyari.com/en/article/8354115

Download Persian Version:

https://daneshyari.com/article/8354115

Daneshyari.com