Acta Physiologiae Plantarum (2019) 41:29
https://doi.org/10.1007/s11738-019-2817-x

ORIGINAL ARTICLE

Silicon mitigates cold stress in barley plants via modifying the activity of apoplasmic enzymes and concentration of metabolites

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Received: 18 December 2017 / Revised: 23 January 2019 / Accepted: 28 January 2019 / Published online: 6 February 2019

Abstract

Apoplasm is the first compartment encountering environmental stresses and is important for plant's tolerance to low temperature. The effect of silicon (Si) on tolerance to low-temperature stress, e.g., chilling and freezing, has been shown in some plant species, while the involvement of leaf apoplasm in the Si-mediated amelioration of cold stress has not been investigated to date. In this work, one winter and one spring barley (*Hordeum vulgare* L.) cultivars were grown without or with Si (56 mg L^{-1} as Na_2SiO_3) and exposed to gradual temperature decrease from +25 to +5 °C for cold acclimation and then treated with freezing (− 5 °C) temperatures. Growth inhibition, photosynthesis reduction, and loss of membrane integrity under low-temperature conditions were higher in the spring than in the winter cultivars, but these parameters were similarly alleviated by Si in both cultivars. Cold acclimation decreased the lethal temperature (LT_{50}) and increased survival (%) of plants exposed to freezing temperatures. The effect of acclimation treatment on reduction of LT_{50} was substituted completely by Si in both cultivars, while in the case of survival rate, Si substituted for acclimation treatment only in the winter cultivar. The activity of antioxidative enzymes and concentrations of soluble carbohydrates and proteins in the leaf apoplasm were increased upon cold acclimation and particularly on Si treatment; the highest values were observed in Si–cold-acclimated plants. Our data demonstrated an ameliorative effect of Si under both chilling and freezing stresses in barley via modification of biochemical properties in the leaf apoplasm.

Keywords Leaf apoplasm · Cold acclimation · Freezing survival · Antioxidative defense · Silicon · Lethal temperature (LT_{50}) · Barley cultivars

Introduction

Silicon (Si) as the second most common element in the lithosphere is not a necessary nutrient for higher plants. However, several beneficial effects on plant growth and metabolism, particularly under different stress conditions, have been observed upon Si application (Hajiboland 2012; Liang et al. 2015; Etesami and Jeong 2018).

Low temperature, including chilling (0–15 °C) and freezing (< 0 °C) temperatures, is one of the most important abiotic stress factors for crop plants. Low temperatures cause multiple adverse effects at the cellular level including membrane damage, production of reactive oxygen species (ROS) and protein denaturation (Janská et al. 2010; Theocharis et al. 2012; Miura and Furumoto 2013). However, gradual exposure to low but non-freezing temperatures increases survival of plants after a freeze–thaw cycle, which is called cold acclimation (Janská et al. 2010). During cold acclimation, numerous physiological, biochemical, and molecular modifications occur in a plant cell, i.e., synthesis of compatible solutes (sugars and amino acids), alteration in the composition of membrane lipids and synthesis of specific proteins (Gusta and Wisniewski 2013).

The apoplasm is the first part of plant cells facing environmental cues. It consists of extracellular aqueous spaces of cell walls, intercellular spaces, and xylem (Clarkson 2007). It has been suggested that the apoplasm contributes not only

Communicated by S. Renault.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11738-019-2817-x) contains supplementary material, which is available to authorized users.

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