



Salicylic acid-induced protection against cadmium toxicity in wheat plants



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ABSTRACT

We have studied the influence of pretreatment of wheat seedlings (*Triticum aestivum* L.) with 50 μ M salicylic acid (SA) on plant resistance to subsequent action of 1 mM cadmium acetate. SA pretreatment decreased the extent of detrimental effect of cadmium on wheat plants, as judged by the decline in the level of stress-induced accumulation of MDA and electrolyte leakage. Furthermore, SA-pretreatment contributed to maintenance of growth characteristics of wheat seedlings at the level close to the control under stress conditions and to acceleration of growth recovery during post-stress period. Detected defense effect of SA may be due to a decline in the amplitude of cadmium-induced accumulation of abscisic acid (ABA) and to reduced fall of indoleacetic acid (IAA) and cytokinins (CK) in stressed plants. In the course of one day treatment, SA activated phenylalanine ammonia-lyase (PAL), the key enzyme of lignin biosynthesis, in roots of seedlings under normal growth conditions contributing to the strengthening of carrier functions of cell walls. This assumption is supported by the data showing significant decline in cadmium accumulation in SA-pretreated plants, especially in the shoots. Cd-treatment was shown to result in accumulation of dehydrins with molecular mass 22, 28, 55 and 69 kDa in wheat seedlings, although low molecular weight dehydrins (22 and 28 kDa) showed greater stress sensitivity. It is noteworthy that SA-pretreatment by itself led to 1.5-fold increase in the content of low molecular weight dehydrins. Nevertheless, SA-pretreated seedlings were characterized by significantly lower Cd-induced accumulation of all of the four dehydrins, apparently due to inhibition of cadmium flow into the plants. The obtained data suggest involvement of dehydrins in the range of defense reactions induced by SA-treatment contributing significantly to development of plant resistance to subsequent action of stress. The use of fluridone allowed us to demonstrate the key role of endogenous ABA in SA-induced changes in the level of dehydrins as well as in the protective effect of SA on wheat plants under cadmium stress resulting from development of defense responses in the course of SA-treatment.

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1. Introduction

Under natural environment, plants experience challenges by adverse conditions, including presence of heavy metals (HM) (Gratão et al., 2005; DalCorso et al., 2008). Due to the progressive contamination of soils with salts of toxic HM, inducing oxidative stress and dehydration in plants and causing not only a decrease in yield, but also a deterioration of its quality, investigation of

the molecular mechanisms of plant resistance to HM acquires special significance (Azevedo et al., 2012; Gallego et al., 2012; Chmielowska-Bąk et al., 2014). Cadmium can be characterized as the most toxic of HM, because it is a non-essential chemical element for the normal functioning and it does not perform any physiological functions in plants (Gratão et al., 2005; Azevedo et al., 2012). Plant response to cadmium is characterized by accumulation of abscisic acid (ABA), stomatal closure, reduced water uptake and flow, inhibition of chlorophyll synthesis and photosynthesis, shifts in the state of pro-/antioxidant cell systems and disturbance of membrane structure integrity resulting from generation of reactive oxygen species (ROS), which in total is reflected in growth and development retardation and decline in plant productivity (Gratão et al., 2009, 2012; Monteiro et al., 2011; Stroiński et al., 2013; Chmielowska-Bąk et al., 2014).

Abbreviations: ABA, abscisic acid; CKs, cytokinins; Flu, fluridone; HM, heavy metal; IAA, indole-3-acetic acid; MI, mitotic index; PAL, phenylalanine ammonia-lyase; SA, salicylic acid.

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By now, a range of proteins is detected involved in plant responses to cadmium including those linked with antioxidant defense, toxic ions chelating and their detoxification (Roth et al., 2006; Ahsan et al., 2009; Monteiro et al., 2011; Wang et al., 2011; Stroiński et al., 2013), as well as proteins implicated in ABA and salicylic acid (SA) signaling (Ahsan et al., 2009; Azevedo et al., 2012; Kang et al., 2012; Chmielowska-Bąk et al., 2014; Asgher et al., 2015), indicating involvement of these stress hormones in the control of plant resistance to cadmium. In fact, cadmium-induced accumulation of ABA (Hsu and Kao, 2003; Stroiński et al., 2013) and SA (Metwally et al., 2003; Han et al., 2013) have been shown to play important role in protection of plants against its toxic effect and plant treatment with ABA (Meng et al., 2009; Asgher et al., 2015) and SA (Hayat et al., 2010; Maslennikova et al., 2013; Asgher et al., 2015) was effective in diminishing the level of growth inhibiting action of cadmium on plants. Seed priming with SA (Shakirova et al., 2003; Krantev et al., 2008) and other phytohormones, e.g., jasmonic acid (Noriega et al., 2012a), has also been shown to be an efficient method for increasing seed vigor as well as seedling growth under stress conditions, however, depending on the hormone concentrations or the nature of stress factors such positive effects may not necessarily occur (Carvalho et al., 2011).

We have shown previously that treatment of wheat seedling with SA under normal conditions results in a fast 1.5-fold reversible increase in ABA, which, however, does not prevent growth promotion by SA, likely due to simultaneous reversible accumulation of indole-3-acetic acid (IAA) without visible changes in cytokinin concentration, while SA-pretreatment prevented salt-stress-induced drop of auxins and cytokinins and maintained elevated level of ABA in seedlings thereby maintaining their growth at the level close to the control (Shakirova et al., 2003). These data indicate a less damaging effect of stress on the SA-pretreated seedlings and the important role of endogenous ABA in the regulation of pre-adaptive and protective action of SA on wheat plants under stress (Shakirova, 2007).

ABA is known to be involved in the control of synthesis of water soluble proteins dehydrins intrinsic to the plant kingdom and joined into group 2 or D 11 of LEA (Late embryogenesis abundant) proteins (Close, 1996; Allagulova et al., 2003; Hanin et al., 2011). Dehydrins are present in almost every cell compartment, while peculiarity of their physico-chemical properties, including indispensable presence of lysine-rich 15-amino acid motif known as K-segment capable of forming secondary structure as amphipathic α -helix enable fulfillment by these proteins of the principally important functions of biopolymers protection from denaturation, membrane stabilization and preservation of cell structure integrity under stress conditions (Close, 1996; Hara, 2010; Hanin et al., 2011; Kosová et al., 2014). Among the dehydration-induced plant proteins, dehydrins characterized by high degree of thermostability and wide range of molecular mass (from 9 to 200 kDa), are most abundant (Close, 1996; Allagulova et al., 2003; Kosová et al., 2014). ABA sensitivity of dehydrin coding genes is determined by the presence in their promoters of ABRE (ABA-responsive)-*cis*-elements containing conservative ACGT sequence capable of binding ABA-activated transcription factors (TFs) from bZIP family (basic leucine zipper) AREB/ABFs (ABA-responsive element-binding/ABA-binding factors) (Allagulova et al., 2003; Hanin et al., 2011). In promoter regions of the genes for dehydrins, there were revealed also other *cis*-regulated elements, such as, e.g., DRE/CRT (dehydration responsive elements/C repeats), determining their sensitivity to drought, strong salinity and cold, but not to ABA and being activated by DREB1/CBF and DREB2 TFs (Allagulova et al., 2003; Hanin et al., 2011; Zhu et al., 2014). There is evidence that the SK₃-type wheat dehydrin *wzy1-2* can be induced not only by osmotic stress, cold and ABA, but also by SA, methyl jasmonate (MeJA) and gibberellic acid (GA), due to the presence in the promoter of this gene

of *cis*-acting regulatory elements, including ABA-, dehydration-, low temperature-, SA-, MeJA-, GA-responsive elements (Zhu et al., 2014). Furthermore, 24-epibrassinolide (Allagulova et al., 2007) has been capable of activating the *TADHN* gene transcription independently of ABA, since seedling treatment with certain concentration of this hormone did not change the content of endogenous ABA. Thus expression of the genes for dehydrins may be regulated by ABA-dependent and ABA-independent signaling pathways (Allagulova et al., 2003, 2007; Hanin et al., 2011; Zhu et al., 2014).

There are literature data showing activation of synthesis and accumulation of dehydrins in plants treated with HM and participation of these proteins in binding and neutralization of ROS, generated in HM-treated plants, as well as in detoxification of toxic ions (Zhang et al., 2006; Xu et al., 2008; Hara, 2010; Hara et al., 2013), which serves as an evidence in favor of important role of dehydrins in development of plant resistance to HM. It has been shown that expression of *PvSR3* gene encoding SKn-type dehydrin was strongly stimulated by HM in leaves of bean seedlings (Zhang et al., 2006). Cadmium has been shown to up-regulate expression of dehydrin genes *DHN1* and *DHN6* in root tips of barley (Tamás et al., 2010), as well as *TADHN* gene of dehydrin in wheat seedlings (Maslennikova et al., 2013).

Present work addresses detection of input of dehydrins into development of SA-induced wheat resistance to toxic action of cadmium ions and importance of endogenous ABA in regulation of this process. Data reported here demonstrate involvement of dehydrins in SA-induced protection of wheat plants against cadmium stress and the key role of SA-induced ABA accumulation in the control of this process.

2. Material and methods

2.1. Plant material and experimental design

Wheat seeds (*Triticum aestivum* L.) of cv. Bashkirskaya 26 were obtained from Chishminsky Crop Production, Bashkortostan, Russia. Wheat seeds were sterilized in 96% ethanol and germinated in trays on filter paper moistened with tap water at an irradiance of 160 $\mu\text{mol}/(\text{m}^2 \text{s})$, 16 h photoperiod, and 21–23 °C temperature. After endosperm excision, the roots of the 3-d-old seedlings were placed into beakers on 2% sucrose. To part of beakers fluridone (Flu), an herbicide reported to block carotenoid biosynthesis by inhibition of phytoene desaturase, effective in reducing the production of abscisic acid in Cd-stressed plants (Stroiński et al., 2013)) was added to yield 5 mg/L concentration. This concentration of Flu was chosen preliminarily as efficiently suppressing stress-induced accumulation of ABA in wheat seedlings (Shakirova et al., 2009). In 3 h, SA was added to part of beakers (with and without fluridone) to yield 50 μM . Exposure to Cd started next day. 4-d-old seedlings were transferred to the mixture of 2% sucrose and cadmium acetate in the presence or absence of Flu for different time periods depending on characteristics measured (indicated below and in figures and tables), but not more than for one day. Plants incubated on 2% sucrose served as a control in all experiments.

2.2. Growth analysis

The growth was assessed by changes in the mitotic activity in the root apical meristems and the increments in fresh and dry weight of wheat seedlings pretreated or untreated with SA and subjected to treatment with cadmium acetate for 8 h. To determine the mitotic activity, root apical meristems of 4-d-old seedlings was fixed in the mixture of acetic acid and ethanol (1:3) for 4 h. After fixation, the plant material was washed with tap water and

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