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Salinity influences the interactive effects of cadmium and zinc on ethylene and polyamine synthesis in the halophyte plant species *Kosteletzkya pentacarpos*

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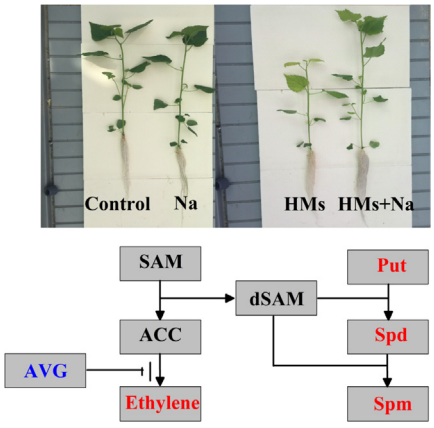
HIGHLIGHTS

- Mixed treatment (Cd + Zn) was more toxic than exposure to single heavy metals (Cd or Zn).
- Leaf senescence was induced by ethylene in response to Cd but not in response to Zn.
- Salinity reduced heavy metal accumulation and improved plant tolerance to Cd and Zn.
- Salinity reduced ethylene synthesis and increased polyamine concentrations.
- Toxicity of Cd + Zn was due to a specific physiological status and not to additive effects.

GRAPHICAL ABSTRACT



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ABSTRACT

Salt marshes are major sinks for heavy metals where plants are often exposed to polymetallic contamination and high salinity. Seedlings from the wetland halophyte plant species *Kosteletzkya pentacarpos* were exposed during three weeks to nutrient solution containing 10 μM $CdCl_2$, 100 μM $ZnCl_2$ or a combination of the two metals (Cd + Zn) in the presence or absence of 50 mM NaCl. Synthesis of the senescing hormone ethylene was quantified together with the concentration of protecting polyamines (spermidine and spermine) and their precursor putrescine and analyzed in relation to senescence markers (soluble protein, malondialdehyde, chlorophyll content and assessment of cell membrane stability). Salinity reduced the deleterious impact of heavy metals on plant growth and decreased accumulation of the pollutants in the plants. Heavy metals increased ethylene synthesis but NaCl decreased it in plants exposed to Cd or to the combined treatment (Cd + Zn) but not in plants exposed to Zn alone. Putrescine increased while spermine and spermidine decreased in Cd-treated plants. Zinc had only a marginal impact on polyamine concentration. The highest putrescine and spermine concentrations were observed in plants exposed to the combined treatment. The inhibitor of ethylene synthesis (AVG; aminovynilglycine) partially restored plant growth, reduced putrescine content and increased spermidine

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and spermine concentration, leading to an attenuation of senescence, mainly in Cd-treated plants. Combined treatment induced a specific physiological status in *K. pentacarpos* which could not be fully explained by an additive effect of Cd and Zn. Results are discussed in relation to specificities of heavy metals impacts on plant response.

1. Introduction

Heavy metals contamination is an important pollution compromising ecosystem stability in several areas in the world (Luo et al., 2017; Meena et al., 2018). Elements such as Cd, Pb, Ni, Cu, Zn, Hg and As induce major risks for human health through contamination of food chain and drinking water (Peralta-Videa et al., 2009; Chowdhury et al., 2016). The situation is especially serious in coastal areas with a high population density. Salt marshes constitute important sinks for the accumulation of heavy metals released by industrial activities (Bai et al., 2012; Mesa et al., 2016). Halophyte plant species have been recommended as an interesting material for phytoremediation purposes (Ruan et al., 2010; Lutts and Lefèvre, 2015). These plants indeed exhibit a fascinating capacity to cope with toxic ions in their environment and salinity has been demonstrated to afford specific advantages in terms of resistance to heavy metals in those species (Ghnaya et al., 2007; Manousaki et al., 2009; Wali et al., 2015, 2016).

Kosteletzkya pentacarpos (formely known as *Kosteletzkya virginica*) is a perennial wetland halophyte plant species from the Malvacea family. This species is a promising plant material for saline agriculture (He et al., 2003). Since several years, however, *K. pentacarpos* is also considered as an interesting plant for phytoremediation purposes. Although the plant is sensitive to copper in the absence of salt, NaCl improves the plant growth in the presence of this toxic element (Han et al., 2012a). A similar observation was reported for Cd and Zn (Han et al., 2012b). In these studies, the recorded salt-induced improvement of heavy metal resistance was related to both a decrease in heavy metal absorption and to an improvement of tolerance mechanisms allowing the plant to cope with the accumulated pollutants. Beside its interest for phytoextraction, *K. pentacarpos* is also a promising species for rhizofiltration approaches and salinity may improve the root properties in relation to Cd and Zn biosorption (Lutts et al., 2016).

The putative interest of a given plant species for phytoextraction of toxic ions depends on the maintenance of the growing processes allowing biomass production and on tolerance mechanisms allowing heavy metal accumulation in the shoot harvestable parts (Buscaroli, 2017). Both processes may be influenced by the hormonal status of the stressed plants. Indeed, plant survival and growth may be hampered by stress-induced senescence frequently occurring as a result of ethylene oversynthesis (Koyama, 2014). Han et al. (2013) demonstrated that Cd exposure increased the synthesis of 1-aminocyclopropane-1-carboxylic acid (ACC; the immediate precursor of ethylene) in *K. pentacarpos*, but ethylene synthesis itself was not measured. According to these authors, salinity contributed to delaying Cd-induced senescence in relation to a decrease in ACC synthesis and an increase in endogenous antioxidant.

Beside ethylene, polyamines (PAs) also influence senescing processes in plants. Polyamines are small aliphatic amines behaving as polycations at cellular pH. They assume a wide range of crucial functions in plant growth and development, from seed germination to flowering processes (Tiburcio et al., 2014; Vera-Sirera et al., 2010). They are also directly involved in plant responses to abiotic and biotic stresses (Fariduddin et al., 2013; Pál et al., 2015; Liu et al., 2015). Polyamines contribute to protein and DNA protection, stabilization of biological membranes and other cellular structures, as well as scavenging of reactive oxygen species (ROS) (Gupta et al., 2013, 2016; Tiburcio et al., 2014). Polyamines interact with cell wall components and lignification processes (Vera-Sirera et al., 2010; Bala et al., 2016). They also assume key functions in the regulation of mineral nutrition and ion homeostasis (Pottosin and Shabala, 2014; Schachtman, 2015). The diamine putrescine (Put) is produced either from ornithine or arginine. Subsequent addition of aminopropyl groups provided by decarboxylated S-adenosylmethionine (dSAM) induces the synthesis of the triamine spermidine (Spd) and the tetramine spermine (Spm). S-adenosylmethionine (SAM) is also the precursor of ACC and the polyamine and ethylene pathways may thus appear to be competitive. Polyamines (especially Spd and Spm) are thought to exhibit antisenescing properties (Pandey et al., 2000) but this specific point is still controversial (Sobiezczuk-Nowicka, 2017). To the best of our knowledge, these important compounds were never studied in *K. pentacarpos*.

Most studies dealing with the physiological impact of heavy metals in plants, including those which consider the influence of salinity, usually consider one single heavy metal. This may appear as an unrealistic oversimplification of field conditions since polluted sites are almost always contaminated by several heavy metals (Ren et al., 2018). This is especially the case in coastal areas of China which are now facing serious environmental problems in relation to polymetallic contaminations (Chen et al., 2018). Distinct heavy metals may have additive, synergistic or antagonist effects depending on the considered plant species and studied physiological properties (Hesami et al., 2018; Dotaniya et al., 2018). Cadmium and zinc are frequently simultaneously present in contaminated areas and share numerous chemical properties. However, they exhibit distinct levels of toxicity in plants. The plant responses to Cd and Zn are triggered by series of signal transduction pathways and involve a large set of physiological and molecular cues. Some of them are common for Cd and Zn response while others are specific to each pollutant (Lin and Aarts, 2012). The impacts of a mixed toxicity induced by the simultaneous presence of Cd and Zn on ethylene and polyamine synthesis in halophyte species, as well as the influence of salinity on these responses, are poorly documented.

The aim of the present work was to analyze the heavy-metal induced leaf senescence process in *Kozteltskya pentacarpos* exposed to individual heavy metals (Cd or Zn) or to combined treatment (Cd + Zn) in the presence or absence of NaCl. Ethylene synthesis and polyamines profile were quantified for plants exposed to treatment during three weeks in nutrient solution. An additional set of experiments was performed in the presence of an inhibitor of ethylene synthesis (aminovinylglycine (AVG), a potent inhibitor of ACC synthase) to obtain additional information on the role of ethylene on stress-induced senescence processes in *K. pentacarpos*.