ISSN: 2348-1900
Plant Science Today
http://horizonepublishing.com/journals/index.php/PST

Review Article

Cadmium stress tolerance in plants: a key role of endogenous and exogenous salicylic acid

Aïcha Belkadhi[*], Wahbi Djebali, Hédia Hédiji, Wided Chaïbi

Faculty of Sciences of Tunis, Physiology and Biochemistry of Plant Response to Abiotic Stresses Unit, University of Tunis El Manar, 1060, Tunis El Manar, Tunisia

Article history
Received: 5 January 2016
Accepted: 14 February 2016
Published: 18 February 2016

Editor
K. K. Sabu

Publisher
Horizon e-Publishing Group

Corresponding Author
Aïcha Belkadhi
✉ aicha585@yahoo.ca

Abstract

Cadmium (Cd) has become one of the major metal stresses which pose a serious threat to plants and animals. In this context, endogenous and exogenous salicylic acid (SA) could play an important role in mitigating the uptake of the Cd ions and providing immunity to plants against the heavy metal stress. SA enhances the resistance capacity of contaminated plants, which, however, depends on the metal concentration and the duration of the treatment. Moreover, SA is considered as a promising signal molecule for improving the efficiency of phytoremediation, and, consequently, growing of safe crops in metal polluted areas. The recent developments in the probable mechanisms by which SA could enhance the tolerance of plants to heavy metals and how it could have an effect on phytoremediation of Cd from contaminated soils are discussed.

Keywords

Cadmium stress; endogenous salicylic acid; exogenous elicitor; phytoremediation

Belkadhi, A., Djebali, W., Hédiji, H., and Chaïbi, W. 2016. Cadmium stress tolerance in plants: a key role of endogenous and exogenous salicylic acid. *Plant Science Today* 3(1): 48-54. http://dx.doi.org/10.14719/pst.2016.3.1.181

Introduction

Cadmium (Cd) is generally known as the most toxic pollutants in the environment. Furthermore, this heavy metal has a high mobility in soil and is easily absorbed by plant roots (Belkadhi *et al.*, 2015 a). Exogenous application of salicylic acid (SA) on the other hand is able to leach and immobilize Cd in soils (Guo *et al.*, 2007). The enhancement of tolerance to Cd stress in SA-treated plants is well-documented (Choudhury and Panda, 2004; Zhang *et al.*, 2011; Guo *et al.*, 2007, 2013; Li *et al.*, 2014; Belkadhi *et al.*, 2015 a, b). For this, SA induces genes that are responsible for resistance to Cd and have evolved a variety of mechanisms to reduce the stress (Shi and Zhu, 2008). These mechanisms include the complex formation and sequestration of Cd (Metwally *et al.*, 2003; Belkadhi *et al.*, 2012), reduction of metal to less toxic forms, generation of the oxidative stress response, reduced membrane permeability, and a direct removal of the metal (Choudhury and Panda, 2004; Guo *et al.*, 2007; Li *et al.*, 2014; Xu *et al.*, 2015). There is also evidence which suggests that SA is capable of facilitating plant growth and reducing/detoxifying Cd toxicity and could be a promising tool in increasing the phytoremediation efficiency (Singer *et al.*, 2003). Considering this as a basis, Tao *et al.* (2013) studied the role of endogenous SA in plant response to lead (Pb) or Cd by the means of wild-type *Arabidopsis* and its SA producing mutant *snc1*, SA-reducing transgenic line *nahG*, SA signal-blocking *npr1-1*, as well as expression of *nahG* in *snc1* plant (*snc1/nahG*) with a comparable level of SA to the wild-type. The results showed that Pb- or Cd induced phytotoxicity in *Arabidopsis* was intensified by elevated endogenous SA, whereas ameliorated by reduced SA.

Analogously to biotic stress, SA also induces a systemic acquired resistance (SAR) in plants exposed to Cd via SA-dependent signal transduction pathway (Volt *et al.*, 2009). In addition, Cd bioaccumulation induces the synthesis of SA, hydrogen peroxide (H_2O_2), and other essential metabolites that finally cause SAR and the resistance to metal stress (Kovács *et al.*, 2014). In this context, the role of SA in plant defense against Cd stress should be considered. In spite of scarce information on the defensive mechanisms by plants via endogenous production of SA, it is known that exogenous SA application may have the potential to activate inducible plant defense systems (Guo *et al.*, 2007, 2013; Li *et al.*, 2014). There are different ways by which SA application can alleviate the Cd toxicity caused to plants.

For example, presoaking of seeds with SA, reduces the availability and mobility of the metal by enhancing its chelation and detoxification via forming a complex with SH-groups (Belkadhi *et al.*, 2012), its binding with siderophores (Sinha and Mukherjee, 2008), and enhancement of the antioxidant capacity (Radwan, 2012; Belkadhi *et al.*, 2014). SA also reduces indirectly the impact of Cd by the secretion of biologically active substances, such as other plant growth-stimulating hormones (Tamás *et al.*, 2012; Shakirova *et al.*, 2016). The beneficial effects on the plant growth in the presence of Cd have been attributed to SA and may include an osmotic adjustment and stomatal regulation (Krantev *et al.*, 2008), modification of organ morphology (Belkadhi *et al.*, 2013), enhanced uptake of minerals (Drazic et al., 2006), and the alteration of the nitrogen accumulation and metabolism (Koç *et al.*, 2013).

Indirect reduction of cadmium toxicity by salicylic acid

SA could contribute to the plant resistance to Cd stress indirectly by increasing the overall fertility of the contaminated soil and by supplementing nutrients, such as, P, Mg, Ca and Fe to stressed plants (Drazic *et al.*, 2006). As a result of this activity, the growth and health of plants are improved. One of the mechanisms of the plant growth promotion by SA is the synthesis of growth-promoting regulator (Tamás *et al.*, 2014; Shakirova *et al.*, 2016). Besides, the exogenous application of SA facilitated the plants in maintaining their improved growth (Shakirova *et al.*, 2016). Recently, Guan *et al.* (2015) established that a glutathione synthetase (GSHS)-like gene from *Lycium chinense* maybe regulated by Cd-induced endogenous SA. In fact, glutathione accumulation occurred via enhanced LcGSHS gene expression and the SA signaling cascade was implicated in this accumulation. Additionally, the overexpression of LcGSHS in transgenic *Arabidopsis* resulted in improvement of tolerance to Cd stress than wild-types. Pre-treatment of wheat seeds with SA has been reported to ameliorate the effects of Cd-induced heavy metal toxicity via enhanced activities of reactive oxygen species (ROS)-scavenging enzymes (Agami and Mohamed, 2013). Although the authors did not analyze the photosynthetic activities, improved growth parameters were estimated to be related to the improved contents of photosynthetic pigments such as chlorophyll a, b and carotenoids in Cd-treated plants. However, the beneficial effect of SA on leaf structure may be due to the crucial role in cell division and expansion.

In order to enlighten the potential mechanisms underlying SA-mediated improved Cd stress tolerance in plants, this section assesses in a consice manner current reports available on the SA-involvement in ROS-signaling and the modulation of defense responses. Both endogenous and exogenous SA were evidenced to play roles in plant metabolism during defense responses (Kang *et al.*, 2014; Khan *et al.*, 2012; 2015). Moreover, the synchronization of dependent and independent SA-signaling components with ROS-signaling provided an appropriate defense response (Khan *et al.*, 2015). SA can act as a signal for the development of the SAR (Shirasu *et al.*, 1997), and can also induce the activation of a protein kinase (Mikolajczyk *et al.*, 2000). *Arabidopsis thaliana* plants were able to recognize the response of ROS–SA interaction via an opposed action of SA and SA-signaling on apoplastic ROS-signaling (Xu and Brosché, 2014). Furthermore, activation of the SA signaling pathway was involved in the responses to Cd rhizotoxicities in *A. thaliana*, explaining the involvement of this signaling pathway in the tolerance mechanisms (Zhao *et al.*, 2009).

Salicylic acid: Protection against cadmium-induced oxidative stress

The exposure of plants to Cd results in an oxidative stress as showed by protein carbonylation (Djebali *et al.*, 2008), lipid peroxidation (Guo *et al.*, 2007), and ROS production (Djebali *et al.*, 2005; Rodríguez-Serrano *et al.*, 2006; Zhang *et al.*, 2011; Zhang and Chen, 2011; Tamás *et al.*, 2015). Cd could also incite a depletion of glutathione and an inhibition of antioxidative enzymes (Jin *et al.*, 2008). The improvement of the plant ROS-detoxification system by SA can be considered as a promising approach to protect plants from the poisonous effects of Cd stress (Rodríguez-Serrano *et al.*, 2006, Zhang *et al.*, 2011, Belkadhi *et al.*, 2015; Tamás *et al.*, 2015). It is reported that SA is a monophenol that acts as an antioxidant and could complement the deficient antioxidative systems of the plants (Garib and Hegazi, 2010). Both exogenous and endogenous SA mitigate much kind of ROS including hydrogen peroxide (H_2O_2), superoxide anion (O_2^-), hydroxyl radicals ($\cdot OH$), singlet oxygen ($^1O_2$) (Shah and Klessig, 1999). According to Panda and Patra (2007), in Cd stress conditions, SA-treated plants could be protected by maximal stimulation of antioxidant molecules and enzymes such as ascorbate, guaiacol peroxidase (GPX, EC 1.11.1.7), and superoxide dismutase (SOD, EC 1.15.1.1), as compared to untreated plants, indicating stimulation of plant immunity by SA (Yang and Dong, 2014).

Moreover, Sappl *et al.* (2004) approved 20 gluthatione-S-transferase (GST, EC 2.5.1.13) isoforms in *Arabidopsis* cell culture responding to SA treatment with a combination of GST antibody detection, LC-MS/MS analysis of 23–30 kDa proteins and glutathione-affinity chromatography. A decrease in the content of non-protein thiols (NP-SHs) in shoots was likely to be associated with the improved antioxidant enzymes activities in roots due to low metal transport in the above-ground parts of the plant (Belkadhi *et al.*, 2012; 2013). On the other hand, the exogenous application of SA stimulates both the accumulation and production of phenolic compounds by plants, known as antioxidants and chelators of Cd, particularly in the plant roots (Kovácik *et al.*, 2009). Besides, Kovács *et al.* (2014) showed that exposure to Cd induced SA synthesis, especially in the leaves, and that the phenylpropanoid synthesis pathway is accountable for the SA accumulation observed after Cd stress. Although no direct relationship was observed between the primary SA levels and the degree of Cd tolerance, the results suggested that the increase of SA levels in roots of wheat varieties during Cd stress could be related with the enhancement of the inner glutathione cycle, therefore endorsing the antioxidant and metal detoxification systems, which improve Cd stress tolerance in wheat plants. The direct relationship between some SA-associated compounds and protective compounds suggested that SA-related signaling may also play a role in the plant adaptation to the heavy metal stress.

Regulation of the antioxidant metabolism under cadmium stress by salicylic acid

SA-pretreatment was well proven to alleviate the deleterious effects of Cd stress in *Triticum aestivum* (Shakirova *et al.*, 2016) and in *Oryza sativa* and *Cucumis melo* through enhancing the activities of antioxidant enzymes including SOD, CAT, GPX, APX, and GR (Guo *et al.*, 2007; Zhang *et al.*, 2015). Activities of H_2O_2-metabolizing enzymes (such as CAT, POD, and APX) and SOD enzymes were also modulated with exogenous SA in flax roots and leaves exposed to Cd (Belkadhi *et al.*, 2013; Belkadhi *et al.*, 2014). Restriction of Cd-uptake in presence of SA (50 µM) suggests an integration of different signals and SA-enhanced Cd tolerance due to SA-regulated Cd uptake as well as the SA-elevated enzymatic and non-enzymatic antioxidant pool in rice (Singh and Shah, 2015). Ascorbate and glutathione, as redox active compounds have been extensively reported to keep up a homeostatic balance of the cellular redox status, and are involved in protective mechanisms against Cd stress (Anjum *et al.*, 2014, 2015; Noctor *et al.*, 2012; Khan *et al.*, 2015). In Cd-exposed *T. aesticum* varieties, SA-signaling was connected to glutathione-related mechanisms (Kovács *et al.*, 2014). SA-mediated differential regulation of the transcript levels of the gene encoding GSH synthetase (GSHS) enzyme was advocated as a major mechanisms underlying previous role of endogenous SA in Cd tolerance via the regulation of LcGSHS transcript expression levels (Guan *et al.*, 2015).

Although numerous reports showed that SA exogenous application can alleviate oxidative damage caused by Cd on different plant species, the results presented by Zawoznik *et al.* (2007) indicated that endogenous SA acted as a potentiating mediator of the oxidative stress triggered by the exposure to Cd in *Arabidopsis* plants. Transgenic plants expressing the bacterial salicylate hydroxylase gene and as a consequence unable to synthesize SA confirmed no data of being affected by Cd exposure after 5 days of Cd treatment, while wild type plants did. SA (500 µM) improved Cd-tolerance and photosynthetic capacity in hemp (*Cannabis sativa*) by increasing both SOD and POD activities (Shi *et al.*, 2009). In another instance the applied SA-induced SOD activity accompanied an enhancement of Ca^{2+} (a second messenger) in shoots and incited a transient increase in H_2O_2 which in turn was argued to stimulate the activities of many antioxidant enzymes and eventually to diminution in intracellular ROS amounts (Hara *et al.*, 2012). Recently, in *Medicago sativa*, a tight link between Haem oxygenase (EC 1.14.99.3), HO-1-mediated and SA-dependent signaling existed in the alleviation of Cd toxic effects; SA-mediated HO-1 up-regulation was implicated in the induction of antioxidative behavior in the root tissues (Cui *et al.*, 2012). On the other hand, Metwally *et al.* (2003) measured the transcript levels of six genes related to antioxidant defense by semi-quantitative reverse transcriptase (RT)-PCR, which showed the suppression of Cd-induced up-regulation of transcript amounts in the SA presoaked barley samples, however, the transcript of glutathione synthase (GS, EC 6.3.2.3) that was already existent at elevated amounts in the SA-presoaked control but down-regulated in the presence of Cd in the nutrient solution.

Salicylic acid: Importance in phytoremediation technologies

Integration of plant defense activators is a novel approach to development of an integrated strategy in order to phytoremediate Cd contamination in soils that require to be cleaned up. SA in this context may exert positive effects on plants through various mechanisms and is reported to enhance phytoremediation strategy. In fact, SA has been shown to enhance phytoremediation efficiency (Tao *et al.*, 2013). Although, no study has showed that endogenous or exogenous SA alone may improve Cd bioavailability and accumulation (Drazic and Mihailovic, 2005), a comparison between the dye contaminated soil and remediated soil revealed that SA decreased in the leaves in the dye contaminated soil than in remediated soil (Jayanthy *et al.*, 2014). The results also exhibited that the level of SA decreased significantly before remediation and enhanced after remediation in both *Vigna radiata* roots and leaves. Regarding the latter, increasing evidence has demonstrated that exposure to Cd increases endogenous SA contents, and the exogenous application of SA can improve the tolerance of plants to heavy metals, demonstrating that SA is implicated in the responses of plants to the heavy metal stress (Metwally *et al.*, 2003; Horváth *et al.*, 2007; Pál *et al.*, 2006). In addition, Tao *et al.* (2013) showed that high endogenous SA intensified Cd-induced phytotoxicity, while low concentration of SA ameliorated the toxicity, which was further proven by an unclaimed performance of double mutant snc1/nahG plants relative to the snc1 plants with high SA content. However, due to the significant difference of initial levels of endogenous SA in a wide range of plant species (Rivas-San Vicente and Plasencia, 2011); it will eventually be tricky to assess precisely which role was played by SA in response of plants to the heavy metal stress by means of an exogenous application (Gururani *et al.*, 2015).

In parallel, most of the SA-applying studies demonstrated that treatments with SA can enhance Cd tolerance in a wide range of plant species (Guo *et al.*, 2007; Horváth *et al.*, 2007; Pál *et al.*, 2006; Belkadhi *et al.*, 2015 a, b), which means that this signal molecule could play an important role in Cd sequestration and chelation (Metwally *et al.*, 2003). In this context, Hao *et al.* (2012) studied the effect of SA, swine manure, and potassium chloride (KCl) applications, on the growth, uptake and translocation of Cd and zinc (Zn) of *Helianthus annuus* grown on a contaminated soil. The results showed that SA reduced the Cd/Zn ratios in flower of sunflower, while KCl significantly increased the Cd/Zn ratios. Large body of evidence has positively confirmed that both endogenous and exogenous SA are crucial in plant responses toward heavy metal stresses, but their roles in phytoremediation are still ambiguous and further studies are required. Providentially, the method of reverse genetics has been widely facilitated to analyze the SA-related mechanisms, and a number of *Arabidopsis* mutants with gain-of-function or loss-of-function in SA-dependent signaling have been identified (Nawrath *et al.*, 2002; Lu *et al.*, 2003). Although *A. thaliana* is not a hyperaccumulator, it represents an appropriate material used to study metal accumulation and acclimation mechanisms (Halimaa *et al.*, 2014).

Conclusion

Both endogenous and exogenous SA play an imperative role in plant tolerance against Cd stress. Endogenous SA induces plant defense against Cd exposure through various physiological, biochemical and molecular mechanisms. Biochemical basis of SA-induced defense has been established to be very dynamic with profound effect on the stress, thereby allowing the plants to withstand it. Additionally, exogenous SA has been proved advisable in enhancing resistance to Cd stress in many plant species. Another important perspective is its plausible agricultural use for improving crop yield. In addition, SA use in phytoremediation is a new study in the field of plant physiology. Seed priming with SA is the most pragmatic approach for agricultural purposes. An important question of this study was how exogenous SA ensured protection against Cd-induced oxidative stress and regulation of the antioxidant metabolism. Alternatively, the positive effects of SA were related to the expression of specific genes coding for defense-related proteins or enzymes. These results may afford good frameworks for strategies aimed at manipulating plants for increasing Cd content in order to develop crops capable for removing efficiently the heavy metal contaminants from the soils.

Competing Interests

The authors declare that they have no competing interests.

Acknowledgements

We wish to thank authors who contributed to the study exemplified in this article.

References

Agami, R.A., and G.F. Mohamed. 2013. Exogenous treatment with indole-3-acetic acid and salicylic acid alleviates cadmium toxicity in wheat seedlings. *Ecotoxicology and. Environmental Safety* 94:164-171. doi: 10.1016/j.ecoenv.2013.04.013. PMID: 23684274.

Anjum, N. A., S.S. Gill, R. Gill, M. Hasanuzzaman, A.C. Duarte, E. Pereira, I. Ahmad, R. Tuteja R, and Tuteja N. 2014. Metal/metalloid stress tolerance in plants: role of ascorbate, its redox couple and associated enzymes. *Protoplasma* 251: 1265–1283. doi: 10.1007/s00709-014-0636-x. PMID: 24682425.

Anjum N.A., Umar S., Aref I.M., and Iqbal M. 2015. Managing the pools of cellular redox buffers and the control of oxidative stress during the ontogeny of drought-exposed mungbean (*Vigna radiata* L.)-role of sulfur nutrition. *Frontiers in Environmental Science* 2:66. doi: 10.3389/fenvs.2014.00066.

Belkadhi, A., H. Hediji, Z. Abbes, W. Djebali, and W. Chaïbi. 2012. Influence of salicylic acid pretreatment on cadmium tolerance and its relationship with non-protein thiol production in flax root. *African Journal of Biotechnology* 11: 9788-9796. doi: 10.5897/AJB11.2051.

Belkadhi, A., A. De Haro, P. Soengas, S. Obregón, M. E. Cartea, W. Djebali, W. Chaïbi. 2013. Salicylic acid improves root antioxidant defense system and total antioxidant capacities of flax subjected to cadmium. *OMICS: A Journal of Integrative Biology* 17(7): 398-406. doi: 10.1089/omi.2013.0030. PMID: 23758477.

Belkadhi, A., A. De Haro, P. Soengas, S. Obregón, M. E. Cartea, W. Chaïbi, and W. Djebali. 2014. Salicylic acid increases tolerance to oxidative stress induced by hydrogen peroxide accumulation in leaves of cadmium-exposed flax (*Linum usitatissimum* L.). *Journal of Plant Interactions* 9(1): 647–654. doi: 10.1080/17429145.2014.890751.

Belkadhi A., A. De Haro, S. Obregon, W. Chaïbi, W. Djebali. 2015. Positive effects of salicylic acid pretreatment on the composition of flax plastidial membrane lipids under cadmium stress. *Environmental Science and Pollution Research* 22 (2): 1457-1467. doi: 10.1007/s11356-014-3475-6. PMID: 25163565.

Belkadhi A., A. De Haro, S. Obregon, W. Chaïbi, and W. Djebali. 2015. Exogenous salicylic acid protects phospholipids against cadmium stress in flax (*Linum usitatissimum* L.). *Ecotoxicology and Environmental Safety* 120: 102-109. doi: 10.1016/j.ecoenv.2015.05.028. PMID: 26057076.

Belkhadi, A., H. Hediji, Z. Abbes, I. Nouairi, Z. Barhoumi, M. Zarrouk, W. Chaïbi, and W. Djebali. 2010. Effects of exogenous salicylic acid pre-treatment on cadmium toxicity and leaf lipid content in *Linum usitatissimum* L. *Ecotoxicology and Environmental Safety* 73: 1004-1011. doi: 10.1016/j.ecoenv.2015.05.028. PMID: 26057076.

Choudhury, S., and S.K. Panda. 2004. Role of salicylic acid in regulating cadmium induced oxidative stress in *Oryza sativa* L. roots. *Bulgarian Journal of Plant Physiology* 30: 95–110.

Cui, W., L. Li, Z.Z. Gao, H.H. Wu, Y. Xie, and W. Shen. 2012. Haem oxygenase-1 is involved in salicylic acid-induced alleviation of oxidative stress due to cadmium stress in *Medicago sativa*. *Journal of Experimental Botany* 63: 5521–5534. doi: 10.1093/jxb/ers201. PMID: 22915740.

Djebali , W., M. Zarrouk, R. Brouquisse, S. El Kahoui, F. Liman, M.H. Ghorbel, and W. Chaïbi. 2005. Ultrastructure and lipid alterations induced by cadmium in tomato *Lycopersicon esculentum* chloroplast membranes. *Plant Biology* 7: 258–368. doi: 10.1055/s-2005-837696. PMID: 16025408.

Djebali, W., P. Gallusci, C. Polge, L. Boulila, N. Galtier, P. Raymond, W. Chaibi, and R. Brouquisse. 2008. Modifications in endopeptidase and 20S proteasome expression and activities in cadmium treated tomato *Solanum lycopersicum* L. plants. Planta 227: 625-639. doi: 10.1007/s00425-007-0644-6. PMID: 17952456.

Drazic, G., and N. Mihailovic. 2005. Modification of cadmium toxicity in soybean seedlings by salicylic acid. *Plant science* 168: 511-517. doi: 10.1104/pp.102.018457. PMID: 166972.

Drazic, G., N. Mihailovic, and M. Lojic. 2006. Cadmium accumulation in *Medicago sativa* seedlings treated with salicylic acid. *Biologia Plantarum* 50: 239–244. doi: 10.1007/s10535-006-0013-5.

Gharib, F.A., A.Z. Hegazi. 2010. Salicylic acid ameliorates germination, seedling growth, phytohormone and enzymes activity in bean (*Phaseolus vulgaris* L.) under cold stress. *Journal of American Science* 6(10): 675-683. doi: 10.3389/fpls.2015.00462. PMID: 4485163.

Guan, C., J. Ji, C. Jia, W. Guan, X. Li, C. Jin, and G. Wang. 2015. A GSHS-like gene from *Lycium chinense* maybe regulated by cadmium induced endogenous salicylic acid and overexpression of this gene enhances tolerance to cadmium stress in Arabidopsis. *Plant Cell Reports* 34: 871–884. doi: 10.1007/s00299-015-1750-8. PMID: 25627256.

Guo, B., Y.C. Liang, Y.G. Zhu, and F.J. Zhao. 2007. Role of salicylic acid in alleviating oxidative damage in rice roots (*Oryza sativa*) subjected to cadmium stress. *Environmental Pollution* 147: 743–749. doi:10.1016/j.envpol.2006.09.007. PMID: 17084493.

Guo, Q., L. Meng, P.C. Mao, Y.Q. Jia, and Y.J. Shi. 2013. Role of exogenous salicylic acid in alleviating cadmium-induced toxicity in *Kentucky bluegrass*. *Biochemical Systematics and Ecology* 50: 269–276. doi:10.1016/j.bse.2013.05.002.

Gururani, M.A., J. Venkatesh, M. Ganesan, R.J. Strasser, Y. Han, J.I. Kim, H.I. Lee, and P.S. Song. 2015. *In vivo* assessment of cold tolerance through chlorophyll-a fluorescence in transgenic zoysiagrass expressing mutant phytochrome A. *PLoS ONE* 10: e0127200. doi: 10.1371/journal.pone.0127200. PMID: 4444231.

Halimaa, P., D. Blande, M.G. Aarts, M. Tuomainen, A. Tervahauta, and S. Kärenlampi. 2014. Comparative transcriptome analysis of the metal hyperaccumulator *Noccaea caerulescens*. *Frontiers in Plant Science* 5: 213. doi: 10.3389/fpls.2014.00213. PMID: 4033236.

Hara, M., J. Furukawa, A. Sato, T. Mizoguchi, and K. Miura. 2012. Abiotic stress and role of salicylic acid in plants. In: Ahmad P, Parsad MNV (eds) Abiotic stress responses in plants: metabolism, productivity and sustainability. Springer Science, New York, 235–251. doi: 10.1007/978-1-4614-0634-1_13.

Horvath, E., G. Szalai, and T. Janda. 2007. Induction of abiotic stress tolerance by salicylic acid signaling. *Journal of Plant Growth Regulation* 26: 290–300. doi: 10.3389/fpls.2015.00462. PMID: 4485163.

Jayanthy, V., R. Geetha, R. Rajendran, P. Prabhavathi, S. Karthik Sundaram, S. Dinesh Kumar, and P. Santhanam. 2014. Phytoremediation of dye contaminated soil by *Leucaena leucocephala* (subabul) seed and growth assessment of *Vigna radiata* in the remediated soil. *Saudi Journal Biological Sciences* 21(4): 324-333. doi: 10.1016/j.sjbs.2013.12.001. PMID: 25183943.

Jin, X., X. Yang, E. Islam, D. Liu, and Q. Mahmood. 2008. Effects of cadmium on ultrastructure and antioxidative defense system in hyperaccumulator and non-hyperaccumulator ecotypes of *Sedum alfredii Hance*. *Journal of*

Hazardous Materials 156 (1–3): 387–397. doi: 10.1016/j.jhazmat.2007.12.064. PMID: 18242844.

Kang, G., G. Li, and T. Guo. 2014. Molecular mechanism of salicylic acid-induced abiotic stress tolerance in higher plants. *Acta Physiologiae Plantarum* 36: 2287–2297. doi: 10.1007/s11738-014-1603-z.

Khan, N. A., R. Nazar, N. Iqbal, and N.A. Anjum. 2012. Phytohormones and Abiotic Stress Tolerance in Plants. Berlin: Springer. doi: 10.1007/978-3-642-25829-9.

Khan, M.I.R., M. Fatma, T.S. Per, N.A. Anjum, and N.A. Khan. 2015. Salicylic acid-induced abiotic stress tolerance and underlying mechanisms in plants. *Frontiers in Plant Science* 6: 462. doi: 10.3389/fpls.2015.00462. PMID: 4485163.

Koç, E., Üstün, A.S., and N. Çelik. 2013. Effect of exogenously applied salicylic acid on cadmium chloride-induced oxidative stress and nitrogen metabolism in tomato (*Lycopersicon esculentum* L.). *Turkish Journal of Biology* 37: 361–369. doi: 10.3906/biy-1211-13.

Kováčik, J., B. Klejdus, J. Hedbavny, and M. Bačkor. 2009. Salicylic acid alleviates NaCl-induced changes in the metabolism of *Matricaria chamomilla* plants. *Ecotoxicology* 18: 544–554. doi: 10.1007/s10646-009-0312-7. PMID: 19381803.

Kovács, V., O.K. Gondor, G. Szalai, I. Majláth, T. Janda and M. Pál. 2014. UV-B radiation modifies the acclimation processes to drought or cadmium in wheat. *Environmental and Experimental Botany* 100: 122–131. doi:10.1016/j.envexpbot.2013.12.019.

Krantev, A., R. Yordanova, T. Janda, G. Szalai, L. and Popova. 2008. Treatment with salicylic acid decreases the effect of cadmium on photosynthesis in maize plants. *Journal of Plant Physiology* 165: 920-931. doi:10.1016/j.jplph.2006.11.014. PMID: 17913285.

Li, X., L. Ma, N. Bu, Y. Li, and L. Zhang. 2014. Effects of salicylic acid pre-treatment on cadmium and/or UV-B stress in soybean seedlings. *Biologia Plantarum* 58: 195-199. doi: 10.1007/s10535-013-0375-4.

Lu, H., D.N. Rate, J.T. Song, and J.T. Greenberg. 2003. ACD6, a novel ankyrin protein, is a regulator and an effector of salicylic acid signaling in the Arabidopsis defense response. *Plant Cell* 15: 2408-2420. doi: 10.1105/tpc.015412. PMID: 14507999.

Metwally, A., I. Finkemeier, M. Georgi, and K.J. Dietz. 2003. Salicylic acid alleviates the cadmium toxicity in barley seedlings. *Plant Physiology* 132 : 272-281. doi: 10.1104/pp.102.018457. PMID: 12746532.

Mikolajczyk, M., O.S. Awotunde, G. Muszynska, D.F. Klessig, and G. Dobrowolska. 2000. Osmotic stress induced rapid activation of a salicylic acid-induced protein kinase and a homolog of protein kinase ASK1 in tobacco cells. *Plant Cell* 12: 165–178. doi: 10.1105/tpc.12.1.165. PMID: 149182.

Nawrath, C., S. Heck, N. Parinthawong, and J.P. Metraux. 2002. EDS5, an essential component of salicylic acid-dependent signaling for disease resistance in Arabidopsis, is a member of the MATE transporter family. *Plant Cell* 14:275–86. doi: 10.1105/tpc.010376. PMID: 150564.

Noctor, G., A. Mhamdi, S. Chaouch, Y. Han, J. Neukermans, B. Marquez-Garcia, G. Queval, and C.H. Foyer. 2012. Glutathione in plants: an integrated overview. *Plant Cell and Environment* 35: 454–484. doi: 10.1111/j.1365-3040.2011.02400.x. PMID: 21777251.

Pál, M., E. Horváth, T. Janda, E. Páldi, and G. Szalai. 2006. Physiological changes and defense mechanisms induced by cadmium stress in maize. *Journal of Plant Nutrition and Soil Science* 169: 239– 246. doi: 10.1002/jpln.200520573.

Panda, S.K., and Patra HK. 2007. Effect of salicylic acid potentiates cadmium-induced oxidative damage in *Oryza sativa* L. leaves. *Acta Physiologiae Plantarum* 29: 567–575. doi: 10.1007/s11738-007-0069-7.

Radwan, D.E.M. 2012. Salicylic acid induced alleviation of oxidative stress caused by clethodim in maize (*Zea mays* L.) leaves. *Pesticide Biochemistry and Physiology* 102: 182-188. doi:10.1016/j.pestbp.2012.01.002.

Rivas-San Vicente, M., and J. Plasencia. 2011. Salicylic acid beyond defence: its role in plant growth and development. *Journal of Experimental Botany* 62: 3321–38. doi: 10.1093/jxb/err031. PMID: 21357767.

Rodriguez-Serrano, M., M.C. Romero-Puertas, G.M. Pastori, F.J. Corpas, L.M. Sandalio, L.A. Del Rio, and J.M. Palma. 2007. Peroxisomal membrane manganese superoxide dismutase: characterization of the isozyme from watermelon (*Citrullus lanatus* Schrad.) cotyledons. *Journal of Experimental Botany* 58: 2417–2427. doi: 10.1093/jxb/erm095. PMID: 17545229.

Sappl, P.G., L. Onate-Sanchez, K.B. Singh, and A.H. Millar. 2004. Proteomic analysis of glutathione *S*-transferases of Arabidopsis thaliana reveals differential salicylic acid-induced expression of the plant-specific phi and tau classes. *Plant Molecular Biology* 54: 205–219. doi: 10.1023/B:PLAN.0000028786.57439.b3. PMID: 15159623.

Shah, J., and D.F. Klessig. 1999. Salicylic acid: signal perception and transduction. In: Hooykaas, P.J.J., M.A. Hall, K.R. Libbenga, eds. Biochemistry and molecular biology of plant hormones. Amsterdam: Elsevier Science Publications 513–541. doi: 10.1016/S0167-7306(08)60503-7.

Shakirova, F.M., C.R. Allagulova, D.R. Maslennikova, E.O. Klyuchnikova, A.M. Avalbaev, and M.V. Bezrukova. 2016. Salicylic acid-induced protection against cadmium toxicity in wheat plants. *Environmental and Experimental Botany* 122: 19–28. doi:10.1016/j.envexpbot.2015.08.002.

Shi, G.R., Q.S. Cai, Q.Q. Liu, and L. Wu. 2009. Salicylic acid-mediated alleviation of cadmium toxicity in hemp plants in relation to cadmium uptake, photosynthesis, and antioxidant enzymes. *Acta Physiologiae Plantarum* 31: 969–977. doi: 10.1007/s11738-009-0312-5.

Shi, Q., and Z. Zhu. 2008. Effects of exogenous salicylic acid on manganese toxicity, element contents and antioxidative system in cucumber. *Environmental and Experimental Botany* 63: 317–326. doi:10.1016/j.envexpbot.2007.11.003.

Shirasu, K., H. Nakajima, V.K. Rajasekhar, R.A. Dixon, and C. Lamb. 1997. Salicylic acid potentiates an agonist-dependent gain control that amplifies pathogen signals in the activation of defense mechanisms. *Plant Cell* 9: 1-10. doi: 10.1105/tpc.9.2.261. PMID: 9061956.

Sing, I., and K. Shah. 2015. Evidences for suppression of cadmium induced oxidative stress in presence of sulphosalicylic acid in rice seedlings. *Plant Growth Regulation* 76: 99–110. doi: 10.1007/s10725-015-0023-4.

Singer, A.C., D.E. Crowley, and I.P. Thompson. 2003. Secondary plant metabolites in phytoremediation and biotransformation. *Trends Biotechnology* 21: 123. doi: 10.1016/S0167-7799 (02)00041-0. PMID: 12628369.

Sinha, S., and S.K. Mukherjee. 2008. Cadmium-induced siderophore production by a high Cd-resistant bacterial strain relieved Cd toxicity in plants through root colonization. *Current Microbiology* 56: 55–60. doi: 10.1007/s00284-007-9038-z. PMID: 17899260.

Tao, S., L. Sun, C. Ma, L. Li, G. Li, and L. Hao. 2013. Reducing basal salicylic acid enhances Arabidopsis tolerance to lead or cadmium. *Plant and Soil* 372: 309–318. doi: 10.1007/s11104-013-1749-2.

Tamas, L.., B. Bočová, J. Huttová, L. Liptáková, I. Mistrík, K. Valentovičová, and V. Zelinová 2012. Impact of the auxin signaling inhibitor p-chlorophenoxyisobutyric acid on short-term Cd-induced hydrogen peroxide production and growth response in barley root tip. *Journal of Plant Physiology* 169 : 1375–1381. doi: 10.1016/j.jplph.2012.05.023. PMID: 22795748.

Tamas, L., I. Mistrik, A. Alemayehu, V. Zelinova, B. Bocova, and J. Huttova. 2015. Salicylic acid alleviates cadmium-induced stress responses through the inhibition of Cd-induced auxin-mediated reactive oxygen species production in barley root tips. *Journal of Plant Physiology* 173 : 1–8. doi: 10.1016/j.jplph.2014.08.018. PMID: 25462072.

Vlot, A.C., D.M.A. Dempsey, and D.F. Klessig. 2009. Salicylic acid, a multifaceted hormone to combat disease. *Annual Review of Phytopathology* 47: 177-206. doi: 10.1146/annurev.phyto.050908.135202. PMID: 19400653.

Xu, E., and M. Brosché. 2014. Salicylic acid signaling inhibits apoplastic reactive oxygen species signaling. *BMC Plant Biology* 14:155. doi: 10.1186/1471-2229-14-155. PMID: 24898702.

Xu, L. L., Z.Y. Fan, Y.J. Dong, J. Kong, and X.Y. Bai. 2015. Effects of exogenous salicylic acid and nitric oxide on physiological characteristics of two peanut cultivars under cadmium stress. *Biologia Plantarum* 59: 171-182. doi: 10.1007/s10535-014-0475-9.

Yan, S., and X. Dong. 2014. Perception of the plant immune signal salicylic acid. *Current Opinion of Plant Biology* 20: 64–68. doi: 10.1016/j.pbi.2014.04.006. PMID: 24840293.

Zawoznik, M., M.D. Groppa, M.L. Tomaro, and M.P. Benavides 2007. Endogenous salicylic acid potentiates cadmium-induced oxidative stress in *Arabidopsis thaliana*. *Plant Science* 173: 190–197. doi:10.1016/j.plantsci.2007.05.004.

Zhang, W.N., and W.L. Chen. 2011. Role of salicylic acid in alleviating photochemical damage and autophagic cell death induction of cadmium stress in *Arabidopsis thaliana*. *Photochemical and Photobiological sciences* 10: 947-955. doi: 10.1039/c0pp00305k. PMID: 21336371.

Zhang, F., H. Zhang, Y. Xia, G. Wang, L. Xu, and Z. Shen. 2011. Exogenous application of salicylic acid alleviates cadmium toxicity and reduces hydrogen peroxide accumulation in root apoplasts of *Phaseolus aureus* and *Vicia sativa*. *Plant Cell Reports* 30: 1475–1483. doi: 10.1007/s00299-011-1056-4. PMID: 21409549.

Zhang, Y., S. Xu, S. Yang, and Y. Chen. 2015. Salicylic acid alleviates cadmium-induced inhibition of growth and photosynthesis through up-regulating antioxidant defense system in two melon cultivars (*Cucumis melo* L.). *Protoplasma* 252: 911–924. doi: 10.1007/s00709-014-0732-y. PMID: 25398649.

Zhao, C.R., T. Ikka, Y. Sawaki, Y. Kobayashi, Y. Suzuki, T. Hibino, S. Sato, N. Sakurai, D. Shibata, and H. Koyama. 2009. Comparative transcriptomic characterization of aluminium, sodium chloride, cadmium and copper rhizotoxicities in *Arabidopsis thaliana*. *BMC Plant Biology* 9: 32. doi: 10.1186/1471-2229-9-32. PMID: 19309492.