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Expression of Genes Involved in Phenolics and Lignin Biosynthesis in *Zinnia elegans* under Saline Stress

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Abstract. Salinization is a common type of agricultural land degradation. It causes inhibition of plant growth and productivity. Previous research into mechanisms of plant resistance to salinity and other stressors has shown that one of nonspecific responses is cell wall lignification which limits translocation of water and ions in the tissues and the whole plant. The current study aims to investigate the responses of *Zinnia elegans* Jacq. grown under regular soil irrigation with 50 mM NaCl. Plant growth parameters and biochemical characteristics, such as the level of hydrogen peroxide and malondialdehyde (MDA), and phenolics and lignin content, were determined. The level of expression of genes encoding the biosynthesis of phenolic compounds and lignin was evaluated by the relative number of transcripts. Application of 50 mM NaCl to soil decreased plant growth and induced lipid peroxidation in stem tissues, despite an increase in the concentration of phenolic compounds. It means that the antioxidant potential of produced phenolics might be insufficient for plant protection. The amount of lignin in stem tissues increased mainly due to Klason lignin which is known to limit cell elongation. The concentration of phenolic compounds correlated with the expression of *PAL*, *C4H* and *4CL* genes involved in their biosynthesis; and the amount of lignin correlated with the expression level of *CCR*, *CAD*, *PRX*, and *LAC* genes.

Keywords: cell wall, hydrogen peroxide, phenolics, lignin, salinization.

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Экспрессия генов метаболизма фенолов и лигнина в *Zinnia elegans* в условиях засоления

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Аннотация. Засоление – распространенный вид нарушения сельскохозяйственных земель. Оно вызывает угнетение роста и продуктивности растений. Изучение механизмов устойчивости растений к засолению показало, что лигнификация клеточной стенки – одна из неспецифических реакций растений на этот и другие стрессоры, что ограничивает транспорт воды и ионов в тканях и целом растении. Настоящее исследование направлено на изучение реакции растений *Zinnia elegans* Jacq. на засоление в длительном эксперименте при выращивании на почве с регулярным поливом 50 мМ NaCl. Определены ростовые характеристики растений и биохимические показатели, такие как уровень пероксида водорода и малонового диальдегида (МДА), содержание фенольных соединений и лигнина. Уровень экспрессии генов, кодирующих биосинтез фенольных соединений и лигнина, оценивали по относительному количеству транскриптов. Внесение 50 mM NaCl в почву подавляло рост растений и индуцировало перекисное окисление липидов в тканях стебля, несмотря на увеличение концентрации фенольных соединений. Вероятно, их антиоксидантного потенциала было недостаточно для защиты растений. Количество лигнина в тканях стебля увеличивалось в основном за счет лигнина Класона, который ограничивал растяжение клеток. Уровень транскриптов генов *PAL*, *C4H*, *4CL*, участвующих в синтезе фенольных соединений, коррелировал с повышением их концентрации; а генов *CCR*, *CAD*, *PRX* и *LAC* – с количеством лигнина.

Ключевые слова: клеточная стенка, пероксид водорода, фенольные соединения, лигнин, засоление.

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Introduction

Land disturbance due to improper agricultural irrigation practices and climate change cause soil salinization (Singh, 2021), which limits plant uptake of water, micro- and macronutrients (Negrao et al., 2017) and decreases crop yields (Cuong et al., 2020; Oliveira et al., 2020). Changes in the water balance of plants can lead to the development of osmotic stress; excess accumulation of Na^+ can have a toxic effect. Under salt stress conditions, an oxidative burst develops in plants, provoking serious changes in photosynthesis, respiration, cell division and expansion, and thus limiting plant growth (Zhao et al., 2021).

Most horticultural (zinnia, impatiens, violet, sage, etc.) (Tenhaken, 2015; García-Caparrós, Lao, 2018) and agricultural (wheat, rice, corn, tomato, etc.) (Cuong et al., 2020; Oliveira et al., 2020; Yasemin et al., 2020; Zhao et al., 2021) plants belong to glycophytes, i.e., are sensitive to salinity. Under conditions of moderate salinity, the synthesis of osmolytes and antioxidants occurs in glycophytes (Yasemin et al., 2020; Zhao et al., 2021), and a number of morphological changes, e.g., an increase in root diameter and cell wall lignification, are observed (Oliviera et al., 2020).

The cell wall is a physical barrier which helps to protect plants from environmental stressors. The content of its main components, i.e., polysaccharides (cellulose, pectin, hemicellulose), phenolic compounds (lignin, suberin) and proteins, varies depending on the tissue type, developmental stage, intensity, and duration of external impacts (Tenhaken, 2015; Byrt et al., 2018; Oliveira et al., 2020; Liu et al., 2021). Secondary cell walls, where lignin and suberin are deposited, contribute to plant salinity resistance (Vaahtera et al., 2019) along with the other mechanisms. Suberin is found mainly in the Casparian strips, and its formation is associated with the activity of NADPH oxidases (Vaahtera et al., 2019). Early suberinization was found in *Arabidopsis thaliana* L. endoderm under salt stress compared to untreated plants; increased deposition of lignin and suberin has been shown in the stele, outer layers of cortical cells, and epiderma in many cereals (Byrt et al., 2018). Lignin makes cell walls rigid and hydrophobic. Its precursors, monolignols (coniferyl, synapyl, caffeyl alcohols), are synthesized in the cytosol via the phenylpropanoid pathway, then transported to the apoplast, where they are oxidized by class III peroxidases (PRX, EC 1.11.1.7) and laccases (LAC, EC 1.10.3.2) into radicals involved in lignin biosynthesis by the free radical mechanism (Veljovic Jovanovic et al., 2018; Berthet et al., 2012).

Phenylpropanoid pathway reactions involve the sequential conversion of phenylalanine to *p*-coumaroyl-CoA (Fraser, Chapple, 2011). Phenylalanine ammonia-lyase (PAL, EC 4.3.1.24) deaminates phenylalanine to cinnamic acid. Then, cinnamate 4-hydroxylase (C4H, EC 1.14.13.11) hydroxylate cinnamic acid to *p*-coumaric acid. 4-coumarate-CoA ligase (4CL, EC 6.2.1.12) catalyzes the synthesis of *p*-coumaroyl-CoA, a precursor of hydroxycinnamic alcohols, flavonoids, lignins, and isoflavonoids (Fraser, Chapple, 2011). Then cinnamoyl-CoA reductase (CCR, EC 1.2.1.44) converts hydroxycinnamoyl-CoA to hydroxycinnamic aldehydes, cinnamyl alcohol dehydrogenase (CAD; EC 1.1.1.195) catalyzes the formation of hydroxycinnamic alcohol, the precursor of *p*-hydroxyphenyl (H),

guaiacyl (G), and syringyl (S) lignin monomers (Fraser, Chapple, 2011). It was shown that high salinity induced lignification of plant cell walls by increased activity of PAL, C4H, 4CL and class III peroxidases (Gupta, De, 2017; Mrazova et al., 2017; Liu et al., 2021).

Z. elegans is a widely cultivated, ornamental plant that is grown for cut flower production and used in landscape design. It is characterized by strong development of mechanical and vascular tissues (Pesquet et al., 2013; Tugbaeva et al., 2021); that is why many experiments were carried out on zinnia as a model plant for studying lignification and xylogenesis (Novo-Uzal et al., 2013; Pesquet et al., 2013). This research aims to study the responses of *Z. elegans* plants including the level of oxidative stress, the accumulation of phenolics and lignin, and the expression of genes involved in their synthesis in a long-term experiment at 50 mM NaCl in the soil substrate.

Materials and methods

In the preliminary experiment aimed at selecting the effective concentrations of NaCl, *Z. elegans* (cv. "Rotkappchen") seeds were germinated on Petri dishes by adding aqueous solutions of 10–200 mM NaCl and distilled water as a control. The linear sizes of the root and hypocotyl of the seedlings were measured on the seventh day. For the long-term experiment, 50 mM NaCl was applied to the soil substrate. The long-term experiments included two variants (treatment with 50 mM NaCl, and controls irrigated with distilled water) with three replicates, each of 25 zinnia plants. All plants were grown individually in 0.2 l pots on a pre-autoclaved substrate – a mixture of peat and coco substrate in a ratio of 3: 1. The peat was neutralized with lime. NH_4NO_3 and KH_2PO_4 were used as fertilizers in the ratio of total N – 1500, P – 2500, K – 3000 mg kg^{-1}. No microelements were added. Pots were irrigated every three days with 30 ml of aqueous solutions 50 mM NaCl for 21 days. In controls, distilled water was used. Plants were grown at 23 °C; the photoperiod was set to 16/8 (day/night). At the start of the experiment, the pH of the substrate mixture was 6.0; $EC_{1:5}$ was 947 μS cm^{-1} in the controls and 1794 μS cm^{-1} in the soil treated with NaCl. At the end of the experiment, $EC_{1:5}$ was 645 μS cm^{-1} in the controls and 2250 μS cm^{-1} in the treated soil. The pH of soil extracts was 5.4 in both variants.

The plants were allowed to grow for three weeks, which corresponds to the middle of the *Z. elegans* vegetative growth phase (Asghar et al., 2022). By that time, the plants had two internodes out of five. The first internode relative to the hypocotyl was completely formed, while the process of xylogenesis was still ongoing in the second one (Pesquet et al., 2013; Tugbaeva et al., 2021). On the 21st day of growth, both treated and untreated plants (30 of each variant) were used to measure root and stem size (length, mm), dry weight (DW), and water content (%). Fresh weight (FW) of plant organs was measured immediately after detachment; DW was determined after fixation at 105 °C for 5 minutes and drying at 70 °C. The water content was calculated as a percentage of fresh weight.

The H_2O_2 content was determined spectrophotometrically in crude extracts obtained from the roots and stems (0.1 M Tris-HCl buffer, pH 7.8) using the method based on the peroxide-mediated oxidation of Fe (II), followed by the reaction of Fe (III) with xylenol orange dye (Bellincampi et al., 2000), and expressed in μM H_2O_2 g^{-1} FW. The lipid peroxidation (LPO) level was estimated spectrophotometrically by the thiobarbituric acid test and expressed in μM MDA g^{-1} FW (Uchiyama, Mihara, 1978). The content of phenolic compounds in 70 % ethanol extracts was determined spectrophotometrically using the Folin-Ciocalteu reagent and expressed

as mg gallic acid equivalent (GAE) per g FW (Larayetan et al., 2019). The Klason lignin (KL) and acid-soluble lignin (ASL) content was determined in dried roots or stems by the sulfuric acid method (Bajpai, 2018) and expressed as a percentage of DW. The optical density of all samples was measured on a Tecan Infinite M200 Pro spectrophotometer (Tecan Austria GmbH, Austria).

Total RNA was extracted from the root and stem tissues using Trizol (TransGen Biotech, China). The concentration and quality of isolated RNA was assessed spectrophotometrically using a NanoDrop ND-1000 instrument (ThermoScientific, USA). For each sample, 100 ng of total RNA was used for the first-strand cDNA synthesis with Oligo(dT)23VN primers and Random Hexamer according to the manufacturer's instructions (HiScriptII 1st standard cDNA synthesis kit, Vasyme, China). The procedure of qRT-PCR and primers used were published earlier (Tugbaeva et al., 2022). The relative expression level was calculated using the $2^{-\Delta\Delta Ct}$ method (Livak, Schmittgen, 2001).

Ten plants of each variant were randomly taken for morphometric analysis in each replicate, 30 individual plants in total. The data are presented as mean values and standard error for all 30 plants.

Biochemical parameters are performed as mean values and standard error for 3 biological replicates (separate experiments) and 5 analytical replicates for each biological replicate, 15 replicates in total. Each of the 5 analytical replicates represented a pooled sample of 10 plants of each variant. Gene expression data were presented as mean values and standard error for 3 biological replicates (separate experiments) and 3 analytical replicates (3 plants) for each biological replicate, totally 9 replicates. Statistical data processing included the Student's *t*-test and Mann-Whitney *U*-test and was carried out using STATISTICA 13 for Windows 10.

Results

In the preliminary experiment, the effect of different NaCl concentrations on the germination of seeds and the growth of *Z. elegans* seedlings was determined. In the case of 10–25 mM NaCl, the root length of seedlings did not change relative to the control group of plants (Fig. 1). Under the conditions of 50 mM NaCl, the root

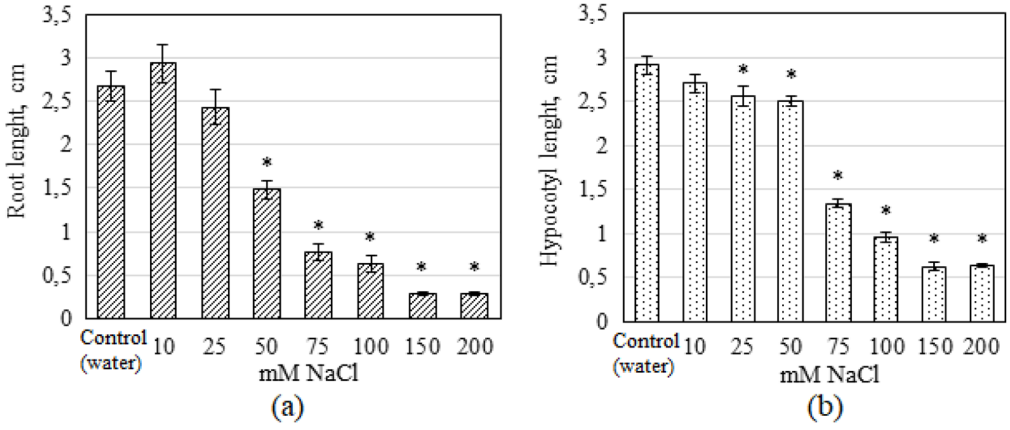

Fig. 1. The root (a) and hypocotyl (b) length of zinnia seedlings on the seventh day of growth under NaCl treatment. Results are expressed as mean ± standard error (n = 30). Asterisks represent significant differences from control (p< 0.05, *t*-test)

length decreased by 44 %, while in the presence of 75–200 mM NaCl, root growth was strongly inhibited. Compared to the control, the hypocotyl height decreased by 12–14 % at 25 and 50 mM NaCl; by 53 and 67 % at 75 and 100 mM NaCl, respectively; by 78 % at 150 and 200 mM NaCl (Fig. 1). For the long-term experiment, 50 mM NaCl was chosen, as it was the minimal concentration that suppressed the growth of both the hypocotyl and the root, the latter more than twice in comparison with the control. In the 21-day experiment, salinization of the substrate with 50 mM NaCl led to a decrease in the linear size and biomass of the axial organs compared with the control. The weight of the root system decreased by 68 %, and the length of the main root by 40 % (Table 1). The stem length decreased by 12 % (Table 1, Fig. 2); and the DW was lower by 42 % relative to the control. The water content did not differ significantly in stem (77.2 % – control and 83.8 % – 50 mM NaCl) and root (94.9 % and 93.0 %, respectively).

The content of LPO product, MDA, a typical marker of stress, increased in all organs of *Z. elegans* plants (by 1.8 times in stem and by 1.5 times in root) in the case of NaCl application to the soil substrate, while the content of hydrogen peroxide as a form of reactive oxygen species increased by 1.9 times in the root and did not change in the stem, compared with the untreated plants (Table 2).

Under stress conditions, plants often accumulate low molecular weight antioxidants, mainly phenolic compounds. In *Z. elegans* roots, the growth of LPO products under increased salinity was accompanied by a slight decrease in

Table 1. Morphological parameters of root and stem of *Z. elegans* plants under NaCl treatment

Variant of experiment	Root length, mm	Root DW, mg	Stem height, mm	Stem DW, mg
Control (water)	13.6 ± 0.5^{a}	135.6 ± 8.8^{a}	57.6 ± 2.1^{a}	43.8 ± 1.9^{a}
Salt treatment (50 mM)	8.1 ± 0.9^{b}	43.3 ± 3.9^{b}	50.6 ± 1.7^{b}	25.0 ± 0.6^{b}

Note. Results are expressed as mean ± standard error (n = 30). Different letters represent significant differences between treatments ($p < 0.05$, t-test).

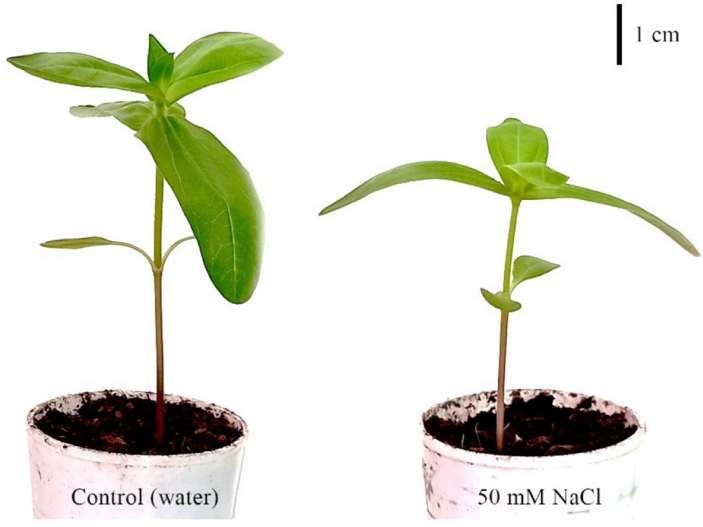

Fig. 2. *Z. elegans* plants (21-days old) under NaCl treatment

Table 2. The content of hydrogen peroxide and MDA, free phenolic compounds, ASL and KL in root and stem tissues of *Z. elegans* under NaCl treatment

Variant	H_2O_2, mg g^{-1} FW		MDA, mg g^{-1} FW		Free phenolic compounds, mg GAE g^{-1} FW		ASL, %		KL, %	
	Root	Stem	Root	Stem	Root	Stem	Root	Stem	Root	Stem
Control (water)	235.8 ± 8.8[a]	120.5 ± 9.1[a]	4.5 ± 0.2[a]	0.31 ± 0.02[a]	0.43 ± 0.01[a]	0.61 ± 0.03[a]	4.89 ± 0.23[a]	6.43 ± 0.11[a]	9.29 ± 0.41[a]	8.02 ± 0.44[a]
Salt treatment (50 mg)	456.1 ± 31.8[b]	139.7 ± 8.1[a]	6.7 ± 0.1[b]	0.87 ± 0.04[b]	0.37 ± 0.02[b]	1.09 ± 0.10[b]	5.07 ± 0.31[b]	5.10 ± 0.30[b]	8.31 ± 0.38[b]	10.60 ± 0.30[b]

Note. Results are expressed as mean ± standard error (n = 15). Different letters represent significant differences between treatments (p< 0.05, U-test).

phenolic compounds. In the stem, on the contrary, it increased by more than 80 % (Table 2).

Phenolic compounds can function not only as antioxidants but also as precursors in lignin biosynthesis. In *Z. elegans* roots, under 50 mM NaCl, the ASL content increased by 16 % compared to the control (Table 2), while the KL content decreased by 12 % relative to the control. In the stem, the amount of ASL decreased by 21 %, and KL increased by 32 % compared to the control.

The expression of genes involved in the phenylpropanoid pathway and lignin biosynthesis in roots and stems was evaluated by the level of their transcripts. In the roots of plants grown under increased salinity, the level of transcripts of the *PAL*, *C4H*, *CCR*, and *CAD* genes decreased, and the *4CL* gene increased by 4.1 times compared to the control (Fig. 3a). The relative expression level of the *PRX* and *LAC* genes also decreased. In stem tissues of *Z. elegans* plants exposed to 50 mM NaCl, the level of expression of the studied genes in the phenylpropanoid pathway increased (Fig. 3): *PAL* by 1.9 times, *C4H* and *4CL* by 1.4–1.5 times, *CCR* by 3.7 times and *CAD* by 9.5 times. The level of expression of the *PRX* and *LAC* genes involved in lignification increased by 2.2 and 2.9 times compared with the control, which corresponded to an increase in the total lignin content in stem tissues in treated plants.

Discussion

Under NaCl excess almost all functions of glycophyte plants change: growth and photosynthesis decrease, water balance and mineral nutrition are disturbed, and a significant part of metabolites are redistributed for the synthesis of antioxidant components (Tenhaken, 2015; Cuong et al., 2020; Zhao et al., 2021). Salt stress leads to a decrease in the biomass and height of ornamental plants (Tenhaken, 2015). It was estimated that in *Z. elegans*, such characteristics as the germination rate, the FW and the size of seedlings and their parts (hypocotyl, cotyledons) decreased under 100 mM NaCl (García-Caparrós, Lao, 2018). In our study, *Z. elegans* plants occurred to be sensitive to salinization of 50 mM NaCl – the root and stem length and weight decreased, but there were no symptoms of acute salt stress in the form of chlorosis. Perhaps one of the reasons for stem growth limitation was the lignification of cell walls that restricted the ability of cell walls to elongate.

In our study, sodium chloride caused the development of oxidative stress in plants. The lipid peroxidation level and hydrogen peroxide concentration in tissues increased. Similar results

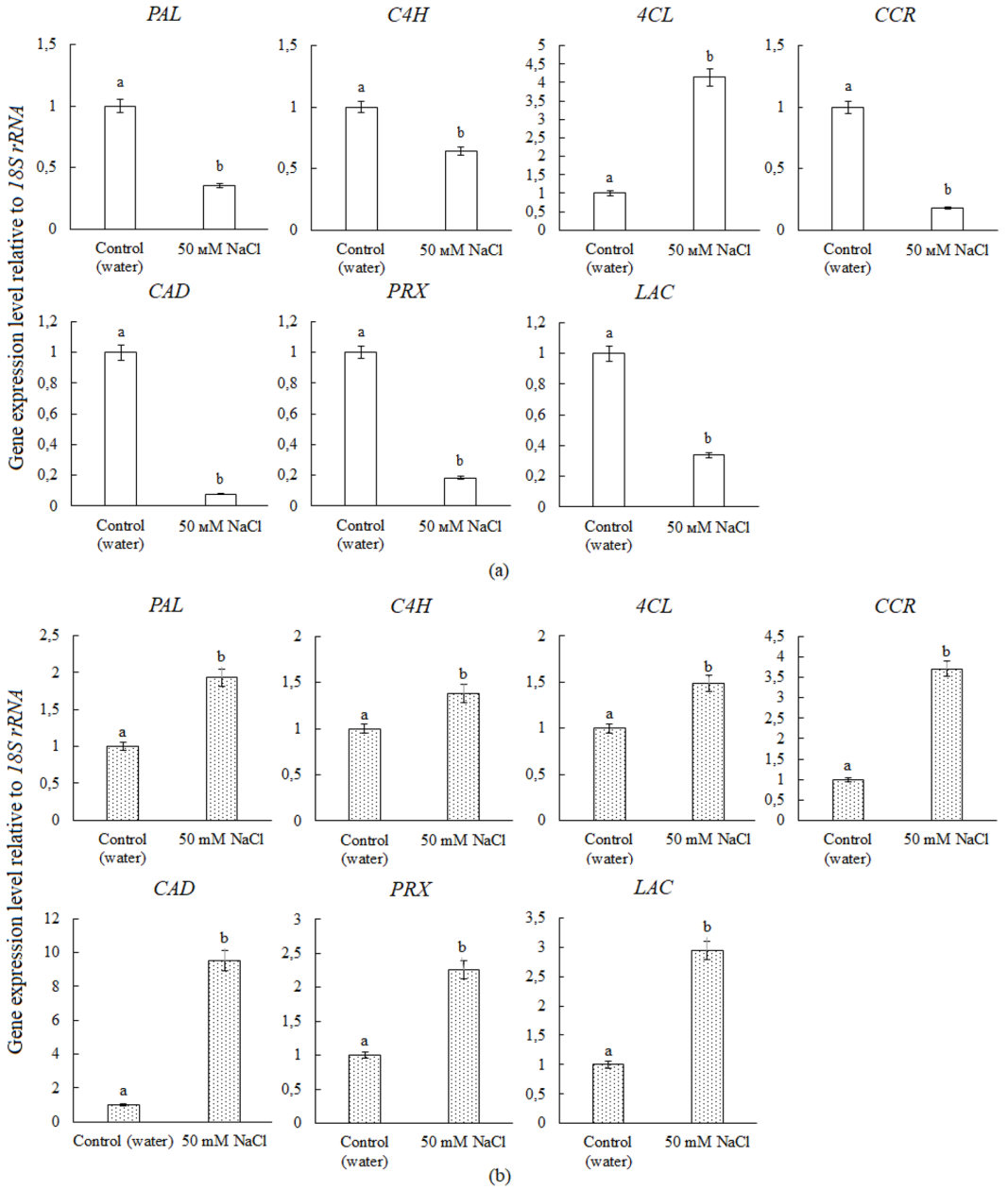

Fig. 3. Relative expression levels of phenylpropanoid biosynthetic pathway genes in root (a) and stem (b) of 21-day-old *Z. elegans* grown under 50 mM NaCl. *18S rRNA* was used as the reference gene. Results are expressed as mean ± standard error (n = 9). Different letters represent significant differences between treatments (p< 0.05, *U*-test)

in the roots and leaves of *Z. elegans* were obtained by Manivannan et al. (2015) under 50 mM NaCl in the medium and by Yasemin et al. (2021) under 50–200 mM NaCl. So, it can be concluded that the decrease of growth due to oxidative burst is a common response of *Z. elegans* to salinization within 50–200 mM NaCl.

A typical reaction to stress conditions is quenching of reactive oxygen species. Phenolic compounds are known as effective antioxidants.

They demonstrate antioxidant activity under stress caused by various biotic and abiotic factors, including salinity. Therefore, the increase in phenolics content in the stem, found in our study, can be considered as a response of *Z. elegans* to increased salinity (Table 2). The rise of phenolics amount in *Z. elegans* stem can be attributed to an increase in gene expression as a corresponding increase in the amount of gene transcripts involved in the regulation of phenylpropanoid pathway, *PAL*, *C4H*, *4CL*, *CCR*, and *CAD*, was also observed (Fig. 3). The Spearman correlation coefficient between the level of *PAL*, *C4H*, *4CL*, *CCR* transcripts and phenolics concentration was 0.85–0.89. In roots, the concentration of phenolics slightly decreased under 50 mM NaCl, which could be explained by the fall of the levels of *PAL*, *C4H*, *CCR*, and *CAD* gene transcripts.

Phenolics are known as substrates for peroxidases. It was shown that the activity of class III peroxidases, which use phenolics as substrates in many reactions, increased under saline conditions (Su et al., 2020). In our study, the expression level of the *PRX* gene decreased in the root but increased in the stem. The results suggest that the synthesis of phenolic compounds via the phenylpropanoid pathway and their use by peroxidases could compensate for each other, and as a result, the total amount of phenolic compounds did not change drastically.

The changes in the content of phenolics and gene transcripts involved in their biosynthesis may depend on the duration of the stress period. In *Lactuca sativa* L. leaves the content of phenolic compounds decreased upon short-term treatment by 50, 100, and 200 mM NaCl, but did not change after a long-term treatment with 5 mM NaCl compared with the control (Kim et al., 2008). Accumulation of phenolics also depended on the genotype: in the roots and leaves of salt-tolerant *Oryza sativa* L. their concentration varied in a more pronounced way than in salt-sensitive plants (Gupta, De, 2017).

Phenolic compounds perform a variety of functions, such as defense responses, signal compounds, pigment compounds, attractants, and repellents (Cheynier et al., 2013). They are also used as precursors in lignin biosynthesis. It is known that lignification is a nonspecific response of plants to different stressors. It protects cells and preserves their integrity under oxidative stress. In our study, the total lignin amount in the stem increased in the case of 50 mM NaCl application. The enhanced lignification under salinity stress was also shown in *Glycine max* L. (Neves et al., 2010), *Lycopersicon esculentum* Mill. (Sánchez-Aguayo et al., 2004), *T. aestivum* (Jbir et al., 2001), *Z. mays* (Oliveira et al., 2020), etc.

The composition of lignin determines its characteristics and could change under abiotic stressors (Oliveira et al., 2020). Our results have evidenced that under saline conditions, the composition of lignin altered in *Z. elegans* – in the stem the amount of ASL decreased, while KL increased; an opposite pattern was observed in roots (Table 2). It is known that the predominance of S-units is characteristic of ASL, while KL consists of H-, G- and S-units (Yasuda et al., 2001). In stems of *Z. mays*, the number of S-monolignols in lignin increased under salt stress (Oliveira et al., 2020), while in roots of *G. max*, both H- and S-monolignols have risen (Neves et al., 2010). Changes in lignin composition are known to result from a complex, time-related regulation of the enzymes and genes involved in the phenylpropanoid pathway and lignin synthesis – *PAL*, *C4H*, *4CL*, *CCR*, *CAD*, *PRX*, and *LAC* (Mrazova et al., 2017; Cuong et al., 2020). The phenylpropanoid pathway enzymes catalyze a balanced sequence of reactions which lead to formation of H-, G-, and S-units of lignin in equal proportion (Fraser, Chapple, 2011). In our study, the level of gene transcripts changed

differently in the under- and aboveground organs under saline stress compared with the control. In the stem, the level of *CCR* and *CAD* transcripts increased. The enzymes encoded by them are responsible for the late stages of the phenylpropanoid pathway (Fraser, Chapple, 2011) and thus for the synthesis of all monolignol-units (H-, G- and S) that are necessary for KL synthesis. The Spearman correlation coefficient for KL and the level of *PRX*, *LAC*, *CCR* and *CAD* transcripts was 0.74–0.78. The level of root transcripts of *CCR* and *CAD* decreased, which caused the predominance of one type of monolignol units.

We suppose that in the *Z. elegans* stem, the rise of the *PRX* gene expression level under saline conditions may lead to an increase in the total peroxidase activity and tissue lignification. The decline in the *PRX* gene expression level in the root did not provide additional lignin deposition. Multidirectional changes in the expression level of phenolics and lignin synthesis genes were also shown for *T. aestivum* (Cuong et al., 2020) and *Lotus japonicus* L. (Mrázová et al., 2017). In the response to salinity stress, the gene encoding class III peroxidases, for example, *TaPRX-2A*, was differentially expressed in the roots and leaves of *T. aestivum* at 200 mM NaCl (Su et al., 2020). The stress caused by 50 mM NaCl had a different effect on the level of *CsaNAPOD* transcripts in the roots, stems, and leaves of *Cucumis sativus* L. seedlings, which suggests organ-specific (Fan et al., 2014) and species-specific responses to salt stress.

As peroxidases are involved in the biosynthesis of lignin and in preventing the development of oxidative stress by hydrogen peroxide degradation (Tugbaeva et al., 2019), the pattern of their participation in stress responses seems to be intriguing and complicated. Along with *PRX*, the expression level of another gene involved in lignin biosynthesis, *LAC*, changed under sodium chloride treatment.

Thus, the responses of *Z. elegans* to 50 mM NaCl are different for roots and stems, and involve both changes in phenolics content and lignin deposition.

Conclusions

Z. elegans is a floral culture widely used in gardening and landscape design. Like all glycophytes, it showed sensitivity to substrate salinity of 50 mM NaCl in the long-term experiment, as evidenced by oxidative stress (an increase of MDA in stem) and inhibition of growth. An increased expression level of genes encoding enzymes of the phenylpropanoid pathway was shown. It can enhance phenolics synthesis and significantly increase their antioxidant effect. Besides, the observed rise of phenolics can provide more phenylpropanoid radicals for lignin biosynthesis. The rise of *PRX* and *LAC* gene expression levels can lead to the additional deposition of lignin. Lignification enhances the mechanical strength of axial organs and thus can limit acropetal translocation of sodium ions in them, restricting the toxic action of Na^+, thus normalising plant functions and providing plant growth in saline conditions.

Our study makes it possible to consider *Z. elegans* as a promising ornamental plant capable of adapting to soil salinity within 50 mM NaCl. This will expand its cultivation areas to urban landscapes and lands disturbed by improper irrigation.

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