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Analysis of the expression of polyamine biosynthesis genes in nodules of the garden pea (*Pisum sativum* L.) and the effect of exogenous treatment with polyamines on their development

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BACKGROUND: Polyamines are acting as signaling molecules during adaptation to stressful environment and as regulators of plant development. In plants, polyamines are represented mainly by putrescine, spermidine and spermine. The concentration of polyamines in symbiotic nodules of some legumes is 5–10 times higher than in the other organs, which indicates their important role in the formation and functioning of symbiotic nodules.

MATERIALS AND METHODS: We analyzed the expression of genes encoding polyamine biosynthesis enzymes in symbiotic nodules, as well as the effect of exogenous polyamines on the nodule number and the average nodule weight in wild-type SGE plants and symbiotic pea mutants SGEFix$^-$-1 (*sym40-1*) and SGEFix$^-$-2 (*sym33-3*).

RESULTS: The comparable expression level of arginine decarboxylase gene (*PsADC*) was observed in all analyzed nodules, whereas the expression level of ornithine decarboxylase gene (PsODC), was highly increased in nodules of SGEFix$^-$-2 (*sym33-3*) mutant. Treatment of the root system with a 0.1 mM solution of polyamines mixture led to an increase in the average weight of the nodule in wild-type plants and in the SGEFix$^-$-2 (*sym33-3*) mutant plants.

CONCLUSIONS: It was shown that the main pathway of putrescine synthesis in wild-type pea symbiotic nodules is the arginine pathway, while the ornithine pathway is probably associated with activation of plant defense reactions. Polyamines acting, apparently, through ethylene, affect the functioning of the nodule meristem.

Keywords: plant-microbial interactions; symbiotic nodule development; polyamines; putrescine; spermidine; spermine.

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Анализ экспрессии генов синтеза полиаминов в клубеньках гороха посевного (*Pisum sativum* L.) и влияние экзогенной обработки полиаминами на их развитие

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Введение. Концентрация полиаминов в симбиотических клубеньках некоторых бобовых в 5–10 раз превышает их концентрацию в других органах, что указывает на их важную роль в формировании и функционировании симбиотических клубеньков.

Материалы и методы. В рамках данной работы был проведен анализ экспрессии генов, кодирующих ферменты биосинтеза полиаминов, в симбиотических клубеньках, а также изучено влияние экзогенных полиаминов на клубенькообразование у растений линии дикого типа SGE и симбиотических мутантов гороха SGEFix$^-$-1 (*sym40-1*) и SGEFix$^-$-2 (*sym33-3*).

Результаты. Было показано, что основной путь синтеза путресцина в симбиотических клубеньках растений дикого типа — аргининовый, тогда как у мутанта SGEFix$^-$-2 (*sym33-3*) активируется также орнитиновый путь. Обработка корневой системы 0,1 мМ раствором смеси полиаминов приводила к увеличению среднего веса клубенька у растений дикого типа и мутанта SGEFix$^-$-2 (*sym33-3*).

Заключение. Таким образом, полиамины, действуя, по-видимому, через этилен, влияют на функционирование меристемы клубеньков.

Ключевые слова: растительно-микробные взаимодействия; развитие симбиотического клубенька; полиамины; путресцин; спермидин; спермин.

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INTRODUCTION

Polyamines are low-molecular-weight organic cations present in all living organisms [1]. In plants, polyamines serve as signaling compounds for adaptation to negative environmental conditions as well as growth and development regulators. They are represented mainly by putrescine, a diamine; spermidine, a triamine, and spermine, a tetramine. They are found in the cell in the free or conjugated form associated with phenolic acids and other low-molecular-weight compounds, or with macromolecules such as proteins and nucleic acids [2].

The biosynthesis of polyamines is initiated with the formation of putrescine. In mammals and fungi, putrescine is synthesized from ornithine in a reaction catalyzed by ornithine decarboxylase. However, in plants and bacteria, there is an alternative pathway for putrescine biosynthesis, involving its synthesis from arginine in a reaction catalyzed by arginine decarboxylase.

The arginine pathway of biosynthesis is the main pathway in most plants. Polyamines formed from arginine are mainly involved in the processes of cell elongation and plant adaptation to abiotic stresses [3, 4]. Polyamines derived from ornithine are involved in cell proliferation in actively growing plant tissues. It is supposed, that ornithine decarboxylase is localized mainly in the cytoplasm, whereas arginine decarboxylase is localized in the thylakoid membranes of chloroplasts [5–8].

Putrescine is formed through the intermediate agmatine, which is synthesized from arginine (Fig. 1). Putrescine is converted to spermidine and spermine by sequential transfer of aminopropyl groups from decarboxylated S-adenosylmethionine catalyzed by spermidine and spermine synthases (Fig. 1). Aminopropyl groups are formed from methionine, which is first converted to S-adenosylmethionine and than it is decarboxylated in a reaction catalyzed by S-adenosylmethionine decarboxylase (Fig. 1). S-adenosylmethionine is a precursor of both polyamines and ethylene [9].

In plants, polyamines are involved in cell division and elongation, rhizogenesis, morphogenesis, flowering, fruit ripening [10], and aging [11]. Polyamines can stabilize DNA, RNA, chromatin, and cell membranes due to their ability to bind to negatively charged molecules and inhibit lipid peroxidation [12, 13]. Treatment of plants with spermidine or spermine prevents the loss of chlorophyll, stabilizes the molecular composition of thylakoid membranes, and delays aging [14].

Cellular homeostasis of polyamines is maintained by the mutual transition of one form of polyamines to another, which are catalyzed by the enzymes polyamine oxidase and diamine oxidase. Such enzymatic reactions lead to the catabolism of polyamines as well as to the hydrogen peroxide production [15, 16]. Using Cu^{2+} and pyridoxal phosphate as cofactors, diamine oxidase catalyzes the formation of hydrogen peroxide, ammonia, and 4-aminobutanal from putrescine. Polyamine oxidase, bound by non-covalent bonds with flavin adenine dinucleotide, can oxidize spermidine and spermine to form 4-aminobutanal, (3-aminopropyl)-4-aminobutanal, 1,3-diaminopropane, and hydrogen peroxide [15, 16].

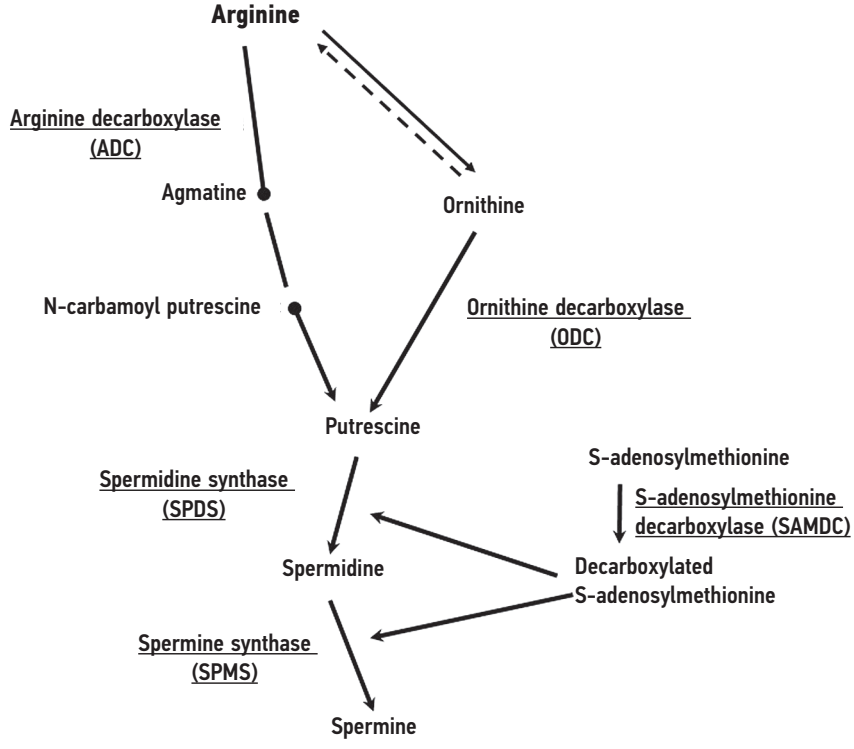

Fig. 1. Pathway of biosynthesis of polyamines in plants. The stages and enzymes are described in the main text

Polyamines also induce NO synthesis [17]. This indicates the important role of these compounds in the metabolism of reactive oxygen and nitrogen species. In addition, putrescine can enhance immune responses triggered by pathogen-associated molecular patterns, leading to an increase in plant resistance to diseases caused by bacterial pathogens [18].

Using genetic approaches, transcriptomics, and metabolomics, the key functions of various polyamines in developmental processes, from flowering to aging, as well as in the regulation of plant resistance to stress, have been identified. Recently, many studies have focused on the effects of exogenous polyamines on the growth and development of fruit and vegetable crops or model plants [19–24]. Attempts to increase the production of endogenous polyamines through genetic manipulation are becoming increasingly popular. However, the mechanisms of the regulation of the biosynthetic and catabolic pathways of polyamines at the transcriptional, translational, and post-transcriptional levels is still largely unknown. The metabolic pathway of polyamines is associated with the pathway of intermediate nitrogen metabolism and other compounds that protect against stress, hormones, and signaling molecules. Further research is required to explore the mechanism of polyamine accumulation to increase plant resistance to stress and regulate their growth. There is still little understanding of the metabolic relationships between polyamines and phytohormones during plant growth and development, especially about the relationship between polyamines and ethylene. Transgenic plants with a modified metabolism of polyamines could be an effective tool for studying the physiological functions of polyamines in higher plants [25–27].

Hydrogen peroxide produced during the catabolism of polyamines is involved in the inhibition of the *Medicago truncatula – Sinorhizobium meliloti* symbiotic system [28]. At the same time, legume nodules accumulate polyamines in concentrations 5–10 times higher than those in roots or leaves [29]. In the nodules of *Lotus japonicus*, the expression of genes involved in the synthesis of spermidine, spermine, and putrescine is induced at the early stages of nodule development and decreases with age. Polyamines accumulate gradually during nodule maturation suggesting their role in division and differentiation of the nodule cells andother functions associated with nitrogen fixation [30, 31]. The role of polyamines in the early stages of infection, their effect on the regulation of nodule development and the efficiency of nitrogen fixation as well as their effect on the bacterial partner for various legumes (*L. japonicus*, *Galega orientalis*, *M. sativa*, and *M. truncatula*) are discussed in detail in reviews [32, 33].

This study is aimed to investigate the role of polyamines at the late stages of the garden pea (*Pisum sativum*) symbiotic nodule formation and functioning. For this purpose, symbiotic mutants of the garden pea are convenient models, as they allow analysis of the role of polyamines in nodule development and in the plant's defense responses during the formation of ineffective symbiosis.

MATERIALS AND METHODS OF RESEARCH

Plant material and bacterial strain

The study used *P. sativum* mutants SGEFix$^-$-1 (*sym40-1*) and SGEFix$^-$-2 (*sym33-3*), which form white ineffective nodules [34], and the original line SGE [35] from the collection of All-Russia Research Institute for Agricultural Microbiology (Table 1). The block of nodule development in the SGEFix$^-$-1 (*sym40-1*) mutant occurs after the release of bacteria into the plant cell [34]. Branched infection threads are formed in the nodules of the SGEFix$^-$-2 (*sym33-3*) mutant, from which bacteria do not release into the cytoplasm of plant cells, but infection droplets are formed in some cells [36] and bacteria can be released [34, 37]. Plants were inoculated with the *Rhizobium leguminosarum* bv. *viciae* 3841 strain [38].

Growing conditions and harvest of material for analysis

The seeds were sterilized with concentrated sulfuric acid for 15 min and washed with sterile water 10 times. The plants were grown in plastic jars containing 100 g

Table 1. Plant material used in the study

Genotype	Mutant allele	Nodule phenotype	References
SGE		Wild-type	[35]
SGEFix$^-$-1	*sym40-1*	Hypertrophied infection droplets, abnormal morphological differentiation of bacteroids, hydrogen peroxide accumulation and oxidative stress inside the nodule, premature degradation of symbiotic structures	[34, 39]
SGEFix$^-$-2	*sym33-3*	'Locked' infection threads and the absence of bacterial release into the host-cell cytoplasm of most infected cells, 'leaky' phenotype	[34, 36, 37]

of sterile vermiculite in an MLR-352H climatic chamber (Sanyo Electric Co., Ltd., Moriguchi, Japan) at the temperature of 21°C, relative humidity of 75%, and illumination of 280 μM photons m^{-2} s^{-1} under a 16/8-hour day and night regime, a nitrogen-free nutrient solution was used to water the plants [40]. To analyze gene expression, nodules (from 10 plants) were harvested 2 and 3 weeks after inoculation (WAI).

The root systems of pea seedlings were treated with a mixture of polyamines (0.1 mM putrescine, spermidine, and spermine) 40 h after inoculation. Further treatments were repeated every other day. The material for the analysis of the effect of polyamines on nodulation was collected after 2 WAIs.

Real-time PCR analysis

The nodules harvested were homogenized in liquid nitrogen. RNA was isolated according to the PureZol Isolation Reagent protocol (Bio-Rad, USA). The concentration and quality of total RNA were determined using the MultiNA microchip electrophoresis system for analysis of nucleic acids (Shimadzu Corporation, Japan). The synthesis of cDNA from 1.5 μg of total RNA treated with DNase I was performed using RevertAid Reverse Transcriptase (MBI Fermentas, Lithuania) in an automatic amplifier C1000™ Thermal Cycler (Bio-Rad, USA). Relative real-time PCR analysis was performed using iQ SYBR Green Supermix (Bio-Rad, USA) according to the protocol in the C1000™ Thermal Cycler automatic amplifier combined with a CFX96™ Real-Time System optical module (Bio-Rad, USA). The expression level was calculated by the $2^{-}\Delta\Delta CT$ method using the reference gene *PsGapC1* (L07500.1) [41]. Primer design was performed using the VectorNTI Advanced 10 software (Invitrogen, USA). The experimental results were processed statistically using the R programming environment and GraphPad Prism software. Statistically significant differences were determined using two-way ANOVA ($p \leq 0.05$).

RESULTS

Analysis of the expression of genes encoding enzymes involved in the biosynthesis of polyamines in nodules of the wild type SGE line and mutants SGEFix⁻-1 (*sym40-1*) and SGEFix⁻-2 (*sym33-3*)

In wild-type plants, the level of transcripts of the *PsADC* gene, encoding arginine decarboxylase, was less in three-week-old nodules than in two-week-old nodules (Fig. 2, *a*). In mutants SGEFix⁻-1 (*sym40-1*) and SGEFix⁻-2 (*sym33-3*), a decrease in the level of transcripts with age was also significant. Nevertheless, the level of *PsADC* transcripts in the SGEFix⁻-1 (*sym40-1*) mutant was significantly higher than that in the wild type at all terms of the analysis, while in the SGEFix⁻-2 (*sym33-3*) mutant, the level of *PsADC* transcripts did not differ from that in the wild type (Fig. 2, *a*).

In wild-type plants, the level of transcripts of the *PsODC* gene, encoding ornithine decarboxylase, did not change with age, in contrast to mutant nodules, where the level of expression in three-week-old nodules was lower than in two-week-old nodules (Fig. 2, *b*). At the same time, active accumulation of *PsODC* transcripts was registered in two-week-old nodules of the SGEFix⁻-2 (*sym33-3*) mutants (Fig. 2, *b*).

The level of transcripts of the *PsSPDS1* gene, encoding spermidine synthase-1, did not change in three-week-old nodules as compared to two-week old nodules in all genotypes analyzed (Fig. 2, *c*), however, the expression level of this gene in mutants SGEFix⁻-1 (*sym40-1*) and SGEFix⁻-2 (*sym33-3*) was higher than that of the wild type at all terms of the analysis.

The level of *PsSPDS2* (spermidine synthase-2) transcripts decreased in three-week-old nodules compared to that in two-week-old nodules (Fig. 2, *d*) of all genotypes. As in the case of *PsSPDS1*, the level of expression of this gene in two-week-old nodules of the SGEFix⁻-1 (*sym40-1*) and SGEFix⁻-2 (*sym33-3*) mutants was higher than that in the wild type.

The level of transcripts of the *PsSAMDC* gene, encoding S-adenosylmethionine decarboxylase involved in the intermediate stage of spermidine synthesis, was higher in mutants than in the wild type (Fig. 2, *e*). In the SGEFix⁻-1 (*sym40-1*) mutant, the level of *PsSAMDC* gene transcripts increased with the age of the nodules, in contrast to the wild type and the SGEFix⁻-2 (*sym33-3*) mutant (Fig. 2, *e*).

Transcripts of the *PsSPMS* gene encoding spermine synthase were not detected at all stages in all genotypes analyzed.

Analysis of nodulation in the wild-type SGE line and mutants SGEFix⁻-1 (*sym40-1*) and SGEFix⁻-2 (*sym33-3*) after treatment with polyamines

In wild-type plants and in the mutant SGEFix⁻-2 (*sym33-3*), in contrast to the SGEFix⁻-1 (*sym40-1*) mutant, the mean weight of the nodules increased when treated with a mixture of 0.1 mM polyamines. But treatment did not affect the number of nodules formed in any of the studied genotypes (Table 2).

DISCUSSION

In the garden pea, arginine decarboxylase is responsible for the biosynthesis of putrescine in ovaries, fruits, and leaves. Arginine decarboxylase activity in the early stages of fruit development correlates with high levels of *PsADC* gene expression in fast-growing tissues [42].

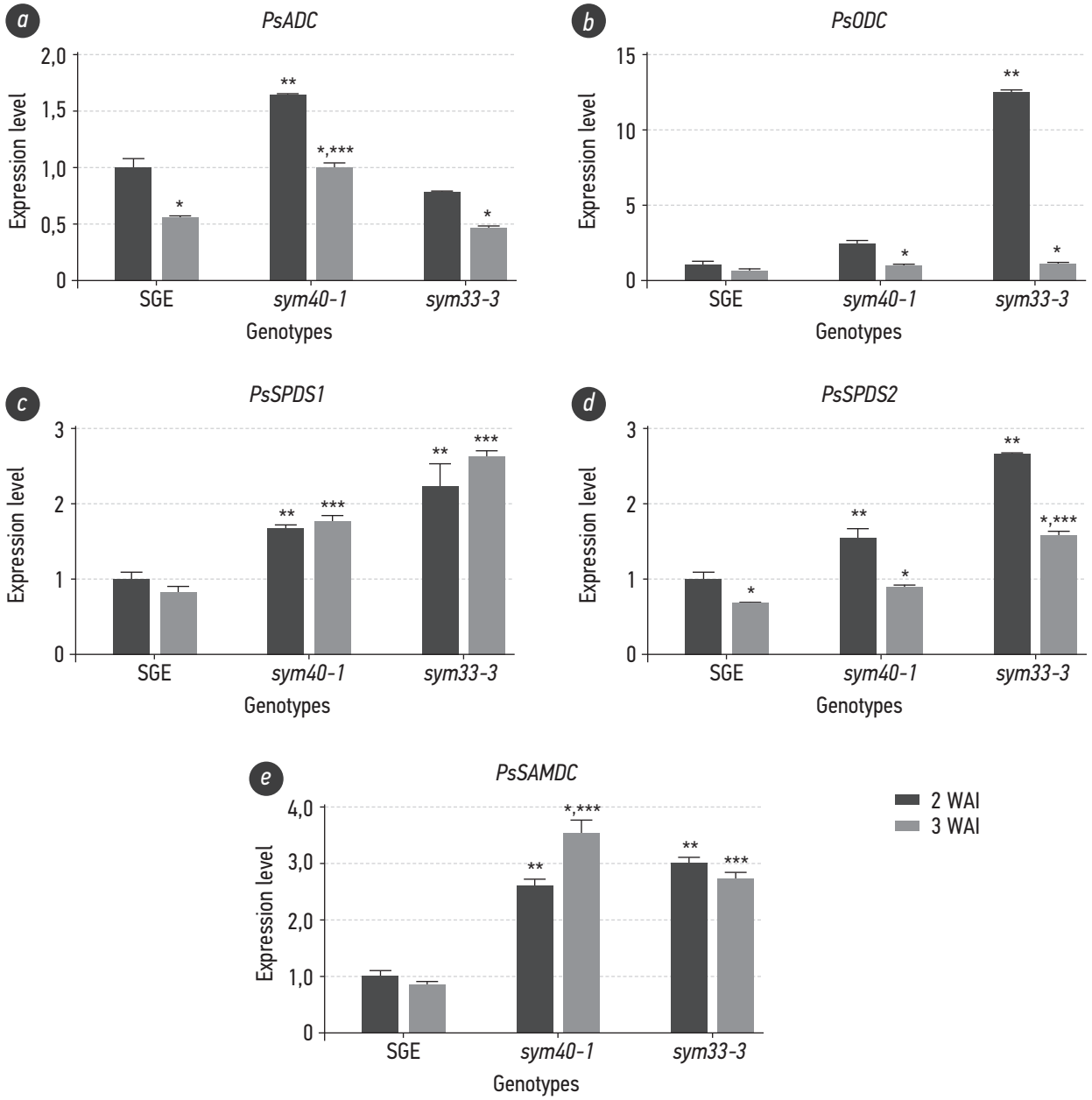

Fig. 2. Level of relative expression of polyamine biosynthesis genes: *a* – *PsADC* gene encoding arginine decarboxylase; *b* – *PsODC* gene encoding ornithine decarboxylase; *c* – *PsSPDS1* gene encoding spermidine synthase-1; *d* – *PsSPDS2* gene encoding spermidine synthase-2; *e* – *PsSAMDC* gene encoding S-adenosylmethionine decarboxylase in two- and three-week old nodules of wild-type garden pea SGE and mutants SGEFix$^-$-1 (*sym40-1*) and SGEFix$^-$-2 (*sym33-3*).* – within the genotype when compared with two-week old nodules; ** – from the wild-type SGE line at week 2 after inoculation (2 WAI); *** – from the wild-type SGE line at week 3 after inoculation (3 WAI); $p \leq 0.05$

The high level of *PsADC* gene transcripts (Fig. 2, *a*), observed in this study in two-week-old wild-type pea nodules, may be associated with active processes of differentiation of infected cells, accompanied by an increase in cell size [43]. In *L. japonicus*, the level of *LjADC* and *LjODC* transcripts was maximal in young 10-day-old nodules and it was decreased with increasing age of the nodules [30]. At the same time, a correlation was observed between the expression of the *LjODC* and *LjADC* genes with the expression of *LjCycD3* encoding the D-type cyclin. In plants, D-type cyclins are involved in the control of the cell cycle, as well as in other plant development programs [44]. Polyamines are more likely to participate in the development of *L. japonicus* nodules than in the process of nitrogen fixation since the transcripts of the gene encoding nitrogenase are found at high levels only after 2 WAI [30].

An increase in the *PsADC* gene expression in the SGEFix$^-$-1 (*sym40-1*) mutant (Fig. 2, *a*) may be associated with the accumulation of hydrogen peroxide and oxidative stress in these nodules [39]. The catabolism of polyamines leads to the formation of hydrogen peroxide and acrolein, which can potentially cause cell damage under stress conditions [15, 16, 45]. However, hydrogen

Table 2. Influence of treatment with 0.1 mM polyamines mixture on the nodulation parameters in the different pea genotypes

Genotype	Average nodule weight, mg		Nodule number	
	Control	Treatment	Control	Treatment
SGE	0.143 ± 0.025	0.192 ± 0.010 *	81.5 ± 10.7	76 ± 10.5
SGEFix⁻-1 (*sym40-1*)	0.037 ± 0.003	0.034 ± 0.001	94 ± 12	100.8 ± 13.5
SGEFix⁻-2 (*sym33-3*)	0.088 ± 0.007	0.172 ± 0.008 **	14.2 ± 1.3	15.1 ± 1.0

*, ** – statistically significant difference of the average nodule dry weight in plants treated with a mixture of polyamines compare with control plants (* $p < 0.05$, ** $p < 0.0001$; Sidak's test).

peroxide is also a signaling molecule that can activate the antioxidant defense system of plants [46]. Indeed, *Zea mays* leaves pretreated with spermine and putrescine showed increased resistance to oxidative stress caused by paraquat [47]. Treatment with exogenous spermidine increased significantly the content of spermidine and spermine and decreased the level of putrescine in the roots of *Cucumis sativus* seedlings under conditions of hypoxic stress. These changes were associated with increased activity of antioxidant enzymes and lower peroxidation of membrane lipids, which ultimately resulted in an increase in plant resistance to hypoxia [48, 49]. Thus, it is likely that polyamines are regulators of redox homeostasis and play a dual role in the oxidative stress of plants [50, 51].

It should also be noted that polyamines are involved in plant protection against pathogenic microorganisms. It has been revealed that treatment with exogenous putrescine of *Arabidopsis thaliana* seedlings induces defense reactions such as callose deposition and an increase in the expression of several marker genes of pattern-activated immunity. These responses are dependent on hydrogen peroxide and NADPH oxidases, thus suggesting that reactive oxygen species mediate signaling triggered by putrescine. Putrescine enhances the responses of pattern-activated immunity due to the production of reactive oxygen species, which leads to an increase in plant resistance to bacterial pathogens [18].

The increased expression level of the *PsSPDS1 and PsSPDS2* genes (Fig. 2, *c, d*) in the nodules of the mutant lines SGEFix⁻-1 (*sym40-1*) and SGEFix⁻-2 (*sym33-3*) may be associated with the participation of polyamines (namely, spermidine) in modulation of defense reactions activated in these nodules [41].

The accumulation of *PsODC* gene transcripts in the SGEFix⁻-2 (*sym33-3*) mutant in two-week-old nodules (Fig. 2, b) may be associated with a strong activation of specific defense reactions in the nodules of this mutant [41, 52] as a result of activation of the ornithine pathway of putrescine biosynthesis besides with arginine pathway.

Treatment with exogenous polyamines did not affect the number of nodules, however it led to an increase in the average nodule weight in the wild-type SGE line and the SGEFix⁻-2 (*sym33-3*) mutant, but not in the SGEFix⁻-1 (*sym40-1*) mutant (Table 2). In previous studies, treatment of *Glycine max* leaf disks with a 1 mM solution of spermidine and spermine increased ethylene production [53]. An increase in ethylene production was also observed when *Oryza sativa* segments were treated with polyamines [54]. At the same time, it was previously demonstrated that exogenous ethylene (added in the form of ethephon) causes an increase in the average nodule weight both in the wild-type SGE line and in the SGEFix⁻-2 (*sym33-3*) mutant [55]. This suggests that the effect of polyamines on nodule weight is mediated by the action of ethylene. The absence of such effect for the nodules of the SGEFix⁻-1 (*sym40-1*) mutant can probably be due to the early cessation of the meristem functioning in such nodules [56], which is manifested in their small size. The high signal level detected during immunolocalization of 1-aminocyclopropane 1-carboxylic acid in the meristematic cells of nodules confirms the importance of ethylene for the meristem functioning [57].

The findings of this study reveal that in the garden pea, the main pathway of putrescine synthesis in effective symbiotic nodules is the arginine pathway. Additionally, in ineffective nodules of the SGEFix⁻-2 (*sym33-3*) mutant, the ornithine pathway is activated, possibly leading to the activation of strong defense reactions in the ineffective nodules of this mutant. Furthermore, polyamines, indirectly through ethylene, seem to affect the nodule meristem functioning.

ADDITIONAL INFORMATION

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REFERENCES

1. Tabor CW, Tabor H. Polyamines. *Ann Rev Biochem*. 1984;53:749–790. DOI: 10.1146/annurev.bi.53.070184.003533

2. Tiburcio AF, Altabella T, Bitrián M, et al. The roles of polyamines during the lifespan of plants: from development to stress. *Planta*. 2014;240(1):1–18. DOI: 10.1007/s00425-014-2055-9

3. Galston AW, Kaur-Sawhney R, Altabella T, et al. Plant polyamines in reproductive activity and response to abiotic stress. *Bot Acta*. 1997;110(3):197–207. DOI: 10.1111/j.1438-8677.1997.tb00629.x

4. Bouchereau A, Aziz A, Larher F, et al. Polyamines and environmental challenges: recent development. *Plant Sci*. 1999;140(2):103–125. DOI: 10.1016/S0168-9452(98)00218-0

5. Borrell A, Culianez-Macia FA, Altabella T, et al. Arginine decarboxylase is localized in chloroplasts. *Plant Physiol*. 1995;109(3):771–776. DOI: 10.1104/pp.109.3.771

6. Walden R, Cordeiro A, Tiburcio AF. Polyamines: small molecules triggering pathways in plant growth and development. *Plant Physiol*. 1997;113(4):1009–1013. DOI: 10.1104/pp.113.4.1009

7. Kakkar RK, Sawhney VK. Polyamine research in plants – a changing perspective. *Physiol Plant*. 2002;116(3):281–292. DOI: 10.1034/j.1399-3054.2002.1160302.x

8. Fuell C, Elliott KA, Hanfrey CC, et al. Polyamine biosynthetic diversity in plants and algae. *Plant Physiol Biochem*. 2010;48(7): 513–520. DOI: 10.1016/j.plaphy.2010.02.008

9. Bitrián M, Zarza X, Altabella T, et al. Polyamines under abiotic stress: metabolic crossroads and hormonal crosstalks in plants. *Metabolites*. 2012;2(3):516–528. DOI: 10.3390/metabo2030516

10. Kakkar RK, Nagar PK, Ahuja PS, et al. Polyamines and plant morphogenesis. *Biol Plant*. 2000;43(1):1–11. DOI: 10.1023/A:1026582308902

11. Pandey S, Ranade SA, Nagar PK, et al. Role of polyamines and ethylene as modulators of plant senescence. *J Bioscie*. 2000;25(3):291–299. DOI: 10.1007/BF02703938

12. Alcázar R, Altabella T, Marco F, et al. Polyamines: molecules with regulatory functions in plant abiotic stress tolerance. *Planta*. 2010;231(6):1237–1249. DOI: 10.1007/s00425-010-1130-0

13. Wimalasekera R, Tebartz F, Scherer GFE. Polyamines, polyamine oxidases and nitric oxide in development, abiotic and biotic stresses. *Plant Sci*. 2011;181(5):593–603. DOI: 10.1016/j.plantsci.2011.04.002

14. Tadolini B. Polyamine inhibition of lipoperoxidation. The influence of polyamines on iron oxidation in the presence of compounds mimicking phospholipid polar heads. *Biochem J*. 1988;249(1):33–36. DOI: 10.1042/bj2490033

15. Cona A, Rea G, Angelini R, et al. Functions of amine oxidases in plant development and defence. *Trends Plant Sci*. 2006;11(2):80–88. DOI: 10.1016/j.tplants.2005.12.009

16. Tavladoraki P, Cona A, Federico R, et al. Polyamine catabolism: target for antiproliferative therapies in animals and stress tolerance strategies in plants. *Amino Acids*. 2012;42(2):411–426. DOI: 10.1007/s00726-011-1012-1

17. Yamasaki H, Cohen MF. NO signal at the crossroads: polyamine-induced nitric oxide synthesis in plants? *Trends Plant Sci*. 2006;11(11):522–524. DOI: 10.1016/j.tplants.2006.09.009

18. Liu C, Atanasov KE, Tiburcio AF, et al. The polyamine putrescine contributes to H_2O_2 and *RbohD/F*-dependent positive feedback loop in *Arabidopsis* PAMP-triggered immunity. *Front Plant Sci*. 2019:894. DOI: 10.3389/fpls.2019.00894

19. De Oliveira LF, Elbl P, Navarro BV, Al E. Elucidation of the polyamine biosynthesis pathway during Brazilian pine (*Araucaria angustifolia*) seed development. *Tree Physiol*. 2016;37:116–130. DOI: 10.1093/treephys/tpw107

20. De Oliveira LF, Navarro BV, Cerruti G, Al E. Polyamines and amino acid related metabolism: the roles of arginine and ornithine are associated with the embryogenic potential. *Plant Cell Physiol*. 2018;59:1084–1098. DOI: 10.1093/pcp/pcy049

21. Mustafavi SH, Badi HN, Sekara A, Al E. Polyamines and their possible mechanisms involved in plant physiological processes and elicitation of secondary metabolites. *Acta Physiol Plant*. 2018;40(6):1–9. DOI: 10.1007/s11738-018-2671-2

22. Agudelo-Romero P, Bortolloti C, Pais MS, Al E. Study of polyamines during grape ripening indicate an important role of polyamine catabolism. *Plant Physiol Biochem.* 2013;67:105–119. DOI: 10.1016/j.plaphy.2013.02.024

23. Pál M, Szalai G, Janda T. Speculation: polyamines are important in abiotic stress signaling. *Plant Sci.* 2015;237:16–23. DOI: 10.1016/j.plantsci.2015.05.003

24. Sequeramutiozabal MI, Erban A, Kopka J, Al E. Global metabolic profiling of *Arabidopsis* polyamine oxidase 4 (*AtPAO4*) loss-of-function mutants exhibiting delayed dark-induced senescence. *Front Plant Sci.* 2016;7:173. DOI: 10.1016/j.plantsci.2015.05.003

25. Kusano T, Berberich T, Tateda C, et al. Polyamines: essential factors for growth and survival. *Planta*. 2008;228(3):367–381. DOI: 10.1007/s00425-008-0772-7.

26. Handa AK, Mattoo AK. Differential and functional interactions emphasize the multiple roles of polyamines in plants. *Plant Physiol Biochem*. 2010;48(7):540–546. DOI: 10.1016/j.plaphy.2010.02.009

27. Chen D, Shao Q, Yin L, et al. Polyamine function in plants: metabolism, regulation on development, and roles in abiotic stress responses. *Front Plant Sci.* 2019;10(9):1945. DOI: 10.3389/fpls.2018.01945

28. Hidalgo-Castellanos J, Marín-Peña A, Jiménez-Jiménez S, et al. Polyamines oxidation is required in the symbiotic interaction *Medicago truncatula – Sinorhizobium meliloti* but does not participate in the regulation of polyamines level under salinity. *Plant Growth Regul*. 2019;88(3):297–307. DOI: 10.1007/s10725-019-00508-z

29. Fujihara S, Abe H, Minakawa Y, et al. Polyamines in nodules from various plant-microbe symbiotic associations. *Plant Cell Physiol*. 1994;35(8):1127–1134. DOI: 10.1093/oxfordjournals.pcp.a078705

30. Flemetakis E, Efrose RC, Desbrosses G, et al. Induction and spatial organization of polyamine biosynthesis during nod-

ule development in *Lotus japonicus*. *Mol Plant Microbe Interact*. 2004;17(12):1283–1293. DOI: 10.1094/mpmi.2004.17.12.1283

31. Efrose RC, Flemetakis E, Sfichi L, et al. Characterization of spermidine and spermine synthases in *Lotus japonicus*: induction and spatial organization of polyamine biosynthesis in nitrogen fixing nodules. *Planta*. 2008;228(1):37–49. DOI: 10.1007/s00425-008-0717-1

32. Jiménez Bremont J, Marina M, Guerrero-González MdL, et al. Physiological and molecular implications of plant polyamine metabolism during biotic interactions. *Front Plant Sci*. 2014;5:95. DOI: 10.3389/fpls.2014.00095

33. Becerra-Rivera VA, Dunn MF. Polyamine biosynthesis and biological roles in rhizobia. *FEMS Microbiol Lett*. 2019;366(7): fnz084. DOI: 10.1093/femsle/fnz084

34. Tsyganov VE, Morzhina EV, Stefanov SY, et al. The pea (*Pisum sativum* L.) genes *sym33* and *sym40* control infection thread formation and root nodule function. *Mol Gen Genet*. 1998;259(5): 491–503. DOI: 10.1007/s004380050840

35. Kosterin OE, Rozov SM. Mapping of the new mutation *blb* and the problem of integrity of linkage group I. *Pisum Genet*. 1993;25:27–31.

36. Tsyganov VE, Seliverstova E, Voroshilova V, et al. Double mutant analysis of sequential functioning of pea (*Pisum sativum* L.) genes *Sym13*, *Sym33*, and *Sym40* during symbiotic nodule development. *Russ J Genet Appl Res*. 2011;1(5):343. DOI: 10.1134/S2079059711050145

37. Voroshilova VA, Boesten B, Tsyganov VE, et al. Effect of mutations in *Pisum sativum* L. genes blocking different stages of nodule development on the expression of late symbiotic genes in *Rhizobium leguminosarum* bv. *viciae*. *Mol Plant Microbe Interact*. 2001;14(4):471–476. DOI: 10.1094/mpmi.2001.14.4.471

38. Glenn AR, Poole PS, Hudman JF. Succinate uptake by free-living and bacteroid forms of *Rhizobium leguminosarum*. *Microbiology*. 1980;119(1):267–271. DOI: 10.1099/00221287-119-1-267

39. Tsyganova AV, Tsyganov VE, Borisov AY, et al. Comparative cytochemical analysis of hydrogen peroxide distribution in pea ineffective mutant SGEFix$^-$1 (*sym40*) and initial line SGE. *Ecological genetics*. 2009;7(3):3–9. (In Russ.) DOI: 10.17816/ecogen733-9

40. Fåhraeus G. The infection of clover root hairs by nodule bacteria studied by a simple glass slide technique. *J Gen Microb*. 1957;16(2):374–381. DOI: 10.1099/00221287-16-2-374

41. Ivanova KA, Tsyganova AV, Brewin NJ, et al. Induction of host defences by *Rhizobium* during ineffective nodulation of pea (*Pisum sativum* L.) carrying symbiotically defective mutations *sym40* (*PsEFD*), *sym33* (*PsIPD3/PsCYCLOPS*) and *sym42*. *Protoplasma*. 2015;252(6):1505–1517. DOI: 10.1007/s00709-015-0780-y

42. Pérez-Amador MA, Carbonell J, Granell A. Expression of arginine decarboxylase is induced during early fruit development and in young tissues of *Pisum sativum* (L.). *Plant Mol Biol*. 1995;28(6):997–1009. DOI: 10.1007/BF00032662

43. Tsyganova AV, Kitaeva AB, Tsyganov VE. Cell differentiation in nitrogen-fixing nodules hosting symbiosomes. *Funct Plant Biol*. 2018;45(2):47–57. DOI: 10.1071/Fp16377

44. Meijer M, Murray JAH. The role and regulation of D-type cyclins in the plant cell cycle. *Plant Mol Biol*. 2000;43(5):621–633. DOI: 10.1023/A:1006482115915

45. Minocha R, Majumdar R, Minocha SC. Polyamines and abiotic stress in plants: a complex relationship. *Front Plant Sci.* 2014;5:175. DOI: 10.3389/fpls.2014.00175

46. Groppa MD, Benavides MP. Polyamines and abiotic stress: recent advances. *Amino Acids*. 2008;34:35–45. DOI: 10.1007/s00726-007-0501-8

47. Durmu N, Kadioglu A. Spermine and putrescine enhance oxidative stress tolerance in maize leaves. *Acta Physiol. Plant.* 2005;27:515–522. DOI: 10.1007/s11738-005-0057-8

48. Jia Y, Guo S, Li J. Effects of exogenous putrescine on polyamines and antioxidant system in cucumber seedlings under root-zone hypoxia stress. *Acta Bot Boreali Occidentalia Sinica*. 2008;28:1654–1662.

49. Wu J, Shu S, Li C, et al. Spermidine-mediated hydrogen peroxide signaling enhances the antioxidant capacity of salt-stressed cucumber roots. *Plant Physiol Biochem.* 2018;128:152–162. DOI: 10.1016/j.plaphy.2018.05.002

50. Bors W, Langebartels C, Michel C, et al. Polyamines as radical scavengers and protectants against ozone damage. *Phytochemistry*. 1989;28(6):1589–1595. DOI: 10.1016/S0031-9422(00)97805-1

51. Saha J, Brauer EK, Sengupta A, Al E. Polyamines as redox homeostasis regulators during salt stress in plants. *Front Environ Sci.* 2015;3:21. DOI: 10.3389/fenvs.2015.00021

52. Tsyganova AV, Seliverstova EV, Brewin NJ, et al. Bacterial release is accompanied by ectopic accumulation of cell wall material around the vacuole in nodules of *Pisum sativum sym33–3* allele encoding transcription factor *PsCYCLOPS*/*PsIPD3*. *Protoplasma*. 2019;256(5):1449–1453. DOI: 10.1007/s00709-019-01383-1

53. Pennazio S, Roggero P. Exogenous polyamines stimulate ethylene synthesis by soybean leaf tissues. *Ann Bot*. 1990;65(1):45–50. DOI: 10.1093/oxfordjournals.aob.a087907

54. Chen SL, Chen CT, Kao CH. Polyamines promote the biosynthesis of ethylene in detached rice leaves. *Plant Cell Physiol*. 1991;32(6):813–819. DOI: 10.1093/oxfordjournals.pcp.a078148

55. Tsyganov VE, Batagov AO, Voroshilova VA, et al. Pea (*Pisum sativum* L.) gene *Sym33* can play a role in ethylene dependent regulation of nodulation. In: Pedrosa FO, Hungria M, Yates G, Newton WE, editors. *Nitrogen Fixation: From Molecules to Crop Productivity Current Plant Science and Biotechnology in Agriculture. 38*. Dordrecht: Springer, 2002. 262 p. DOI: 10.1007/0-306-47615-0_140

56. Voroshilova VA, Demchenko KN, Brewin NJ, et al. Initiation of a legume nodule with an indeterminate meristem involves proliferating host cells that harbour infection threads. *New Phytol*. 2009;181(4):913–923. DOI: 10.1111/j.1469-8137.2008.02723.x

57. Serova TA, Tikhonovich IA, Tsyganov VE. Analysis of nodule senescence in pea (*Pisum sativum* L.) using laser microdissection, real-time PCR, and ACC immunolocalization. *J Plant Physiol*. 2017;212:29–44. DOI: 10.1016/j.jplph.2017.01.012

СПИСОК ЛИТЕРАТУРЫ

1. Tabor C.W., Tabor H. Polyamines // Ann Rev Biochem. 1984. Vol. 53. P. 749–790. DOI: 10.1146/annurev.bi.53.070184.003533

2. Tiburcio A.F., Altabella T., Bitrián M., et al. The roles of polyamines during the lifespan of plants: from development to stress // Planta. 2014. Vol. 240. No. 1. P. 1–18. DOI: 10.1007/s00425-014-2055-9

3. Galston A.W., Kaur-Sawhney R., Altabella T., et al. Plant polyamines in reproductive activity and response to abiotic stress // Bot Acta. 1997. Vol. 110. No. 3. P. 197–207. DOI: 10.1111/j.1438-8677.1997.tb00629.x

4. Bouchereau A., Aziz A., Larher F., et al. Polyamines and environmental challenges: recent development // Plant Sci. 1999. Vol. 140. No. 2. P. 103–125. DOI: 10.1016/S0168-9452(98)00218-0

5. Borrell A., Culianez-Macia F.A., Altabella T., et al. Arginine decarboxylase is localized in chloroplasts // Plant Physiol. 1995. Vol. 109. No. 3. P. 771–776. DOI: 10.1104/pp.109.3.771

6. Walden R., Cordeiro A., Tiburcio A.F. Polyamines: small molecules triggering pathways in plant growth and development // Plant Physiol. 1997. Vol. 113. No. 4. P. 1009–1013. DOI: 10.1104/pp.113.4.1009

7. Kakkar R.K., Sawhney V.K. Polyamine research in plants – a changing perspective // Physiol Plant. 2002. Vol. 116. No. 3. P. 281–292. DOI: 10.1034/j.1399-3054.2002.1160302.x

8. Fuell C., Elliott K.A., Hanfrey C.C., et al. Polyamine biosynthetic diversity in plants and algae // Plant Physiol Biochem. 2010. Vol. 48. No. 7. P. 513–520. DOI: 10.1016/j.plaphy.2010.02.008

9. Bitrián M., Zarza X., Altabella T., et al. Polyamines under abiotic stress: metabolic crossroads and hormonal crosstalks in plants // Metabolites. 2012. Vol. 2. No. 3. P. 516–528. DOI: 10.3390/metabo2030516

10. Kakkar R.K., Nagar P.K., Ahuja P.S., et al. Polyamines and plant morphogenesis // Biol Plant. 2000. Vol. 43. No. 1. P. 1–11. DOI: 10.1023/A:1026582308902

11. Pandey S., Ranade S.A., Nagar P.K., et al. Role of polyamines and ethylene as modulators of plant senescence // J Bioscie. 2000. Vol. 25. No. 3. P. 291–299. DOI: 10.1007/BF02703938

12. Alcázar R., Altabella T., Marco F., et al. Polyamines: molecules with regulatory functions in plant abiotic stress tolerance // Planta. 2010. Vol. 231. No. 6. P. 1237–1249. DOI: 10.1007/s00425-010-1130-0

13. Wimalasekera R., Tebartz F., Scherer G.F.E. Polyamines, polyamine oxidases and nitric oxide in development, abiotic and biotic stresses // Plant Sci. 2011. Vol. 181. No. 5. P. 593–603. DOI: 10.1016/j.plantsci.2011.04.002

14. Tadolini B. Polyamine inhibition of lipoperoxidation. The influence of polyamines on iron oxidation in the presence of compounds mimicking phospholipid polar heads // Biochem J. 1988. Vol. 249. No. 1. P. 33–36. DOI: 10.1042/bj2490033

15. Cona A., Rea G., Angelini R., et al. Functions of amine oxidases in plant development and defence // Trends Plant Sci. 2006. Vol. 11. No. 2. P. 80–88. DOI: 10.1016/j.tplants.2005.12.009

16. Tavladoraki P., Cona A., Federico R., et al. Polyamine catabolism: target for antiproliferative therapies in animals and stress tolerance strategies in plants // Amino Acids. 2012. Vol. 42. No. 2. P. 411–426. DOI: 10.1007/s00726-011-1012-1

17. Yamasaki H., Cohen M.F. NO signal at the crossroads: polyamine-induced nitric oxide synthesis in plants? // Trends Plant Sci. 2006. Vol. 11. No. 11. P. 522–524. DOI: 10.1016/j.tplants.2006.09.009

18. Liu C., Atanasov K.E., Tiburcio A.F., et al. The polyamine putrescine contributes to H_2O_2 and *RbohD/F*-dependent positive feedback loop in *Arabidopsis* PAMP-triggered immunity // Front Plant Sci. 2019. Vol. 10. ID894. DOI: 10.3389/fpls.2019.00894

19. De Oliveira L.F., Elbl P., Navarro B.V., Al E. Elucidation of the polyamine biosynthesis pathway during Brazilian pine (*Araucaria angustifolia*) seed development // Tree Physiol. 2016. Vol. 37. P. 116–130. DOI: 10.1093/treephys/tpw107

20. De Oliveira L.F., Navarro B.V., Cerruti G., Al E. Polyamines and amino acid related metabolism: the roles of arginine and ornithine are associated with the embryogenic potential // Plant Cell Physiol. 2018. Vol. 59. P. 1084–1098. DOI: 10.1093/pcp/pcy049

21. Mustafavi S.H., Badi H.N., Sekara A., Al E. Polyamines and their possible mechanisms involved in plant physiological processes and elicitation of secondary metabolites // Acta Physiol Plant. 2018. Vol. 40. No. 6. P. 1–9. DOI: 10.1007/s11738-018-2671-2

22. Agudelo-Romero P., Bortolloti C., Pais M.S., Al E. Study of polyamines during grape ripening indicate an important role of polyamine catabolism // Plant Physiol Biochem. 2013. Vol. 67. P. 105–119. DOI: 10.1016/j.plaphy.2013.02.024

23. Pál M., Szalai G., Janda T. Speculation: polyamines are important in abiotic stress signaling // Plant Sci. 2015. Vol. 237. P. 16–23. DOI: 10.1016/j.plantsci.2015.05.003

24. Sequeramutiozabal M.I., Erban A., Kopka J., Al E. Global metabolic profiling of *Arabidopsis* polyamine oxidase 4 (*AtPAO4*) loss-of-function mutants exhibiting delayed dark-induced senescence // Front Plant Sci. 2016. Vol. 7. ID173. DOI: 10.1016/j.plantsci.2015.05.003

25. Kusano T., Berberich T., Tateda C., et al. Polyamines: essential factors for growth and survival // Planta. 2008. Vol. 228. No. 3. P. 367–381. DOI: 10.1007/s00425-008-0772-7

26. Handa A.K., Mattoo A.K. Differential and functional interactions emphasize the multiple roles of polyamines in plants // Plant Physiol Biochem. 2010. Vol. 48. No. 7. P. 540–546. DOI: 10.1016/j.plaphy.2010.02.009

27. Chen D., Shao Q., Yin L., et al. Polyamine function in plants: metabolism, regulation on development, and roles in abiotic stress responses // Front Plant Sci. 2019. Vol. 9. ID1945. DOI: 10.3389/fpls.2018.01945

28. Hidalgo-Castellanos J., Marín-Peña A., Jiménez-Jiménez S., et al. Polyamines oxidation is required in the symbiotic interaction *Medicago truncatula — Sinorhizobium meliloti* but does not participate in the regulation of polyamines level under salinity // Plant Growth Regul. 2019. Vol. 88. No. 3. P. 297–307. DOI: 10.1007/s10725-019-00508-z

29. Fujihara S., Abe H., Minakawa Y., et al. Polyamines in nodules from various plant-microbe symbiotic associations // Plant Cell Physiol. 1994. Vol. 35. No. 8. P. 1127–1134. DOI: 10.1093/oxfordjournals.pcp.a078705

30. Flemetakis E., Efrose R.C., Desbrosses G., et al. Induction and spatial organization of polyamine biosynthesis during nodule development in *Lotus japonicus* // Mol Plant Microbe Interact. 2004. Vol. 17. No. 12. P. 1283–1293. DOI: 10.1094/mpmi.2004.17.12.1283
31. Efrose R.C., Flemetakis E., Sfichi L., et al. Characterization of spermidine and spermine synthases in *Lotus japonicus*: induction and spatial organization of polyamine biosynthesis in nitrogen fixing nodules // Planta. 2008. Vol. 228. No. 1. P. 37–49. DOI: 10.1007/s00425-008-0717-1
32. Jiménez Bremont J., Marina M., Guerrero-González Md.L., et al. Physiological and molecular implications of plant polyamine metabolism during biotic interactions // Front Plant Sci. 2014. Vol. 5. ID95. DOI: 10.3389/fpls.2014.00095
33. Becerra-Rivera V.A., Dunn M.F. Polyamine biosynthesis and biological roles in rhizobia // FEMS Microbiol Lett. 2019. Vol. 366. No. 7. ID fnz084. DOI: 10.1093/femsle/fnz084
34. Tsyganov V.E., Morzhina E.V., Stefanov S.Y., et al. The pea (*Pisum sativum* L.) genes *sym33* and *sym40* control infection thread formation and root nodule function // Mol Gen Genet. 1998. Vol. 259. No. 5. P. 491–503. DOI: 10.1007/s004380050840
35. Kosterin O.E., Rozov S.M. Mapping of the new mutation *blb* and the problem of integrity of linkage group I // Pisum Genet. 1993. Vol. 25. P. 27–31.
36. Tsyganov V.E., Seliverstova E., Voroshilova V., et al. Double mutant analysis of sequential functioning of pea (*Pisum sativum* L.) genes *Sym13*, *Sym33*, and *Sym40* during symbiotic nodule development // Russ J Genet Appl Res. 2011. Vol. 1. No. 5. P. 343. DOI: 10.1134/S2079059711050145
37. Voroshilova V.A., Boesten B., Tsyganov V.E., et al. Effect of mutations in *Pisum sativum* L. genes blocking different stages of nodule development on the expression of late symbiotic genes in *Rhizobium leguminosarum* bv. *Viciae* // Mol Plant Microbe Interact. 2001. Vol. 14. No. 4. P. 471–476. DOI: 10.1094/mpmi.2001.14.4.471
38. Glenn A.R., Poole P.S., Hudman J.F. Succinate uptake by free-living and bacteroid forms of *Rhizobium leguminosarum* // Microbiology. 1980. Vol. 119. No. 1. P. 267–271. DOI: 10.1099/00221287-119-1-267
39. Цыганова А.В., Цыганов В.Е., Борисов А.Ю., и др. Сравнительный цитохимический анализ распределения перекиси водорода у неэффективного мутанта гороха SGEFix$^-$1 (*sym40*) и исходной линии SGE // Экологическая генетика. 2009. Т. 7, № 3. С. 3–9. DOI: 10.17816/ecogen733-9
40. Fåhraeus G. The infection of clover root hairs by nodule bacteria studied by a simple glass slide technique // J Gen Microb. 1957. Vol. 16. No. 2. P. 374–381. DOI: 10.1099/00221287-16-2-374
41. Ivanova K.A., Tsyganova A.V., Brewin N.J., et al. Induction of host defences by *Rhizobium* during ineffective nodulation of pea (*Pisum sativum* L.) carrying symbiotically defective mutations *sym40* (*PsEFD*), *sym33* (*PsIPD3/PsCYCLOPS*) and *sym42* // Protoplasma. 2015. Vol. 252. No. 6. P. 1505–1517. DOI: 10.1007/s00709-015-0780-y
42. Pérez-Amador M.A., Carbonell J., Granell A. Expression of arginine decarboxylase is induced during early fruit development and in young tissues of *Pisum sativum* (L.) // Plant Mol Biol. 1995. Vol. 28. No. 6. P. 997–1009. DOI: 10.1007/BF00032662
43. Tsyganova A.V., Kitaeva A.B., Tsyganov V.E. Cell differentiation in nitrogen-fixing nodules hosting symbiosomes // Funct Plant Biol. 2018. Vol. 45. No. 2. P. 47–57. DOI: 10.1071/Fp16377
44. Meijer M., Murray J.A.H. The role and regulation of D-type cyclins in the plant cell cycle // Plant Mol Biol. 2000. Vol. 43. No. 5. P. 621–633. DOI: 10.1023/A:1006482115915
45. Minocha R., Majumdar R., Minocha S.C. Polyamines and abiotic stress in plants: a complex relationship // Front Plant Sci. 2014. Vol. 5. ID175. DOI: 10.3389/fpls.2014.00175
46. Groppa M.D., Benavides M.P. Polyamines and abiotic stress: recent advances // Amino Acids. 2008. Vol. 34. P. 35–45. DOI: 10.1007/s00726-007-0501-8
47. Durmu N., Kadioglu A. Spermine and putrescine enhance oxidative stress tolerance in maize leaves // Acta Physiol Plant. 2005. Vol. 27. P. 515–522. DOI: 10.1007/s11738-005-0057-8
48. Jia Y., Guo S., Li J. Effects of exogenous putrescine on polyamines and antioxidant system in cucumber seedlings under root-zone hypoxia stress // Acta Bot Boreali Occidentalia Sinica. 2008. Vol. 28. P. 1654–1662.
49. Wu J., Shu S., Li C., et al. Spermidine-mediated hydrogen peroxide signaling enhances the antioxidant capacity of salt-stressed cucumber roots // Plant Physiol Biochem. 2018. Vol. 128. P. 152–162. DOI: 10.1016/j.plaphy.2018.05.002
50. Bors W., Langebartels C., Michel C., et al. Polyamines as radical scavengers and protectants against ozone damage // Phytochemistry. 1989. Vol. 28. No. 6. P. 1589–1595. DOI: 10.1016/S0031-9422(00)97805-1
51. Saha J., Brauer E.K., Sengupta A., Al E. Polyamines as redox homeostasis regulators during salt stress in plants // Front Environ Sci. 2015. Vol. 3. ID21. DOI: 10.3389/fenvs.2015.00021
52. Tsyganova A.V., Seliverstova E.V., Brewin N.J., et al. Bacterial release is accompanied by ectopic accumulation of cell wall material around the vacuole in nodules of *Pisum sativum sym33-3* allele encoding transcription factor *PsCYCLOPS*/*PsIPD3* // Protoplasma. 2019. Vol. 256. No. 5. P. 1449–1453. DOI: 10.1007/s00709-019-01383-1
53. Pennazio S., Roggero P. Exogenous polyamines stimulate ethylene synthesis by soybean leaf tissues // Ann Bot. 1990. Vol. 65. No. 1. P. 45–50. DOI: 10.1093/oxfordjournals.aob.a087907
54. Chen S.L., Chen C.T., Kao C.H. Polyamines promote the biosynthesis of ethylene in detached rice leaves // Plant Cell Physiol. 1991. Vol. 32. No. 6. P. 813–819. DOI: 10.1093/oxfordjournals.pcp.a078148
55. Tsyganov V.E., Batagov A.O., Voroshilova V.A., et al. Pea (*Pisum sativum* L.) gene *Sym33* can play a role in ethylene dependent regulation of nodulation. In: Pedrosa F.O., Hungria M., Yates G., Newton W.E., editors. Nitrogen Fixation: From Molecules to Crop Productivity Current Plant Science and Biotechnology in Agriculture. 38. Dordrecht: Springer, 2002. 262 p. DOI: 10.1007/0-306-47615-0_140
56. Voroshilova V.A., Demchenko K.N., Brewin N.J., et al. Initiation of a legume nodule with an indeterminate meristem involves proliferating host cells that harbour infection threads // New Phytol. 2009. Vol. 181. No. 4. P. 913–923. DOI: 10.1111/j.1469-8137.2008.02723.x
57. Serova T.A., Tikhonovich I.A., Tsyganov V.E. Analysis of nodule senescence in pea (*Pisum sativum* L.) using laser microdissection, real-time PCR, and ACC immunolocalization // J Plant Physiol. 2017. Vol. 212. P. 29–44. DOI: 10.1016/j.jplph.2017.01.012

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