

Ph.D. Thesis

**The role of ethylene status in salt stress acclimation of tomato**

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**Szeged**

**2019.**

## Introduction

The gaseous plant hormone ethylene (ET) plays pivotal role in the regulation of several physiological processes of plants, such as photosynthesis or the accumulation of reactive oxygen- (ROF) or nitrogen forms (RNF). Furthermore, ET is a crucial participant of plant abiotic stress responses. Exogenous ET generators have been used in various studies to evaluate the role of ET in these processes. However, the effect of ET precursor, 1-aminocyclopropane-1-carboxylic acid, which could accumulate in the root zone under natural conditions, was rarely investigated. Thus, the concentration- and/or time dependent influence of exogenous ACC on plants, especially on photosynthesis or on the accumulation of reactive molecules mentioned previously is mostly unknown. The actual ET sensitivity or changes in ET level in tissues, which can be defined as ET status of plants, could be important before or during abiotic stress acclimation. Therefore, the identification of specific processes induced by exogenous ACC, which could alter the physiological response during a subsequent abiotic stress are very important.

The abiotic stress induced in plants by high salt concentrations in soil or in irrigation water becomes more significant in the agriculture worldwide with climate change. Thus, the investigation of plant salt stress responses at physiological or molecular level is of great importance. Although ET is an important participant in the regulation of these processes, its effect was mostly investigated during long term salt stress, although the events occurring during the early period of stress acclimation – from hours to few days – determine the fate of the plant later. Furthermore, the data about the connection between plant ET status and ROF/RNF accumulation under short term salt stress are scarce. The role of ET in the regulation of photosynthesis, especially the activity of photosystem I (PSI) under those circumstances mentioned before is barely known.

Hence, during our experiments, we used two approaches. First, we investigated the effect of 0.01, 1.0 and 100  $\mu$ M ACC concentrations applied in hydroponic nutrient solution under non-stress conditions, on major physiological processes of tomato (*Solanum lycopersicum* L.), which could play a role in abiotic stress acclimation such as photosynthesis, ion accumulation as well as ROF and RNF accumulation. The second

approach was divided into two different experimental designs due to technical reasons. Tomato plants with altered ET status, (pre-)treated with 10  $\mu$ M ACC or ET receptor mutant (*Never ripe*), were exposed to a growth retarding but tolerable 100 mM or a lethal, 250 mM NaCl concentrations for 24 hours and sampled at multiple time points. We examined the role of ET in early salt stress response by monitoring the parameters mentioned above, and the activity and expression of the most important antioxidant enzymes, which controls oxidative stress.

## **Aims**

The investigation of concentration- or time dependent effect of ET on plants is very important. ET emission induced by stress – depending on stress-ET concentration – could affect the acclimation process negatively but may also regulate defence mechanisms. While the physiological role of stress-ET has been studied intensively, our knowledge about the direct effects of its precursor, ACC on plants is rare, despite the fact, that ACC could be present in plant root zone in physiologically active concentrations in soil water. Thus, the long-term, time dependent effects of different ACC concentrations on the parameters, which are also important in stress acclimation – e.g. nutrient content, ROF and RNF accumulation, photosynthesis –are mostly unknown. There is also insufficient information about the relation of plant ET status and photosynthetic activity – especially about the regulation of PSI – during the early phase of salt acclimation. Furthermore, the same is the case with ET status dependent ROF and RNF accumulation under short term salt stress. It is also important to note, that the changes in leaf physiology could be interpreted hardly without knowing the changes in the root system.

In the dissertation, we were looking for the answers to the following questions:

1. What is the concentration- and time-dependent effect of enhanced ACC concentrations in the root zone on the water homeostasis, ion accumulation, ROF and RNF production of WT tomato plants?

2. How does enhanced root zone ACC influences the photosynthetic activity of tomato leaves as a function of ACC concentration and treatment time?
3. How could the potential abiotic stress tolerance of tomato plant be related to the increased ACC concentrations in the root zone? While induced systemic resistance (ISR) triggered by non-pathogen microorganisms acts through activating ET signalling, the question may arise: Is it possible that ET/ACC induced physiological changes could influence abiotic stress acclimation?
4. What kind of salt stress related, ET-dependent responses could be observed in the first attack site of salt stress, in the roots?
5. How could be the physiological responses to different salt concentrations modified in tomato plants by blocking of the ET signalization at the receptor level or by the artificially enhanced ACC/ET content of tissues? How does root responses affect leaf physiological processes?
6. What kind of ET status-dependent responses could be identified under sublethal or lethal salt stress in the activity and expression of antioxidant enzymes? What are the differences between the salt responses of roots and leaves in relation with altered ET status?
7. How does ET status of tomato plants influence the activity and regulation of photosystems and CO<sub>2</sub> assimilation during the early period of salt stress?

### **Materials and methods**

Tomato plants (*S. lycopersicum* Mill. L. cvar. Rio Fuego WT, cvar. Ailsa Craig WT and homozygous *Nr/Nr*, ET receptor mutant) were grown hydroponically in controlled environment until they reached 4-7-week-old age, when experiments were performed in two different approaches.

During the first phase of our work, we investigated the effect of elevated ACC concentrations in the root zone of *S. lycopersicum* Mill. L. cvar. Rio Fuego, without the presence of any specific stress factor. We added 0.01  $\mu$ M or 1.0  $\mu$ M ACC (Sigma-Aldrich, St. Louis, MO) – concentrations that could be present under natural conditions

– and 100  $\mu\text{M}$  ACC – concentration that generates ET production in plants equivalent to stress-induced ET – into the nutrient solution, and treated the plants for one week. We monitored the changes of those parameters, which are also important during abiotic stress responses: biomass production, ion accumulation, ROF and RNF contents, sugar content in roots and mature but not senescent leaves, and photosynthetic activity in the leaves.

During the second phase of our experiments, we applied salt treatment with two different strength on tomato plants with different ET status and evaluated the role of ET in the early period of salt stress. For technical reasons, we performed this experiment in two steps, which therefore referred to as experimental setup 2<sup>nd</sup> and 3<sup>rd</sup>. During the former, we used the roots – mostly 1 cm apical segments – of WT and *Nr* mutant in *S. lycopersicum* Mill. L. cv. Ailsa Craig genetic background. Uniform, adventitious roots formed during the rooting of tomato shoots were exposed to sublethal, 100 mM or lethal, 250 mM NaCl concentrations and ROF and RNF production, ion accumulation, cell viability and programmed cell death (PCD) markers were monitored for 24 hours, at multiple time points. In the 3<sup>rd</sup> experimental setup we exposed WT plants, WT plants treated with exogenous ACC or *Nr* mutant *S. lycopersicum* Mill. L. cv. Ailsa Craig cultivar to salt stress. Half of the WT plant population was pre-treated with 10  $\mu\text{M}$  ACC – not too high but surely generates ET – for 1 hour, and after that 100 mM or 250 mM NaCl was added to ACC containing nutrient solution. In this time point, which is considered as starting, 0-time point of the experiment, salt treatment was performed on the rest of WT plants and *Nr* mutants. Sample harvest and measurements took place after the 1<sup>st</sup>, 6<sup>th</sup> and 24<sup>th</sup> hours after the addition of salt.

During our experiments, we evaluated the biomass production of roots and leaves, monitored ET emission with gas chromatograph (Hewlett-Packard 5890 Series II, Hewlett-Packard, Wilmington, USA) and element content with atomic absorption spectroscope (Hitachi Z-8200, Tokyo, Japan; setup 1<sup>st</sup> and 2<sup>nd</sup>) or with ICP-MS (setup 3<sup>rd</sup>). ROF and RNF accumulation and cell viability were measured with fluorescent microscopy (Zeis Axiowert 200M, Carl Zeiss Inc., Jena, Germany) and biochemical methods ( $\text{H}_2\text{O}_2$  or  $\text{O}_2^-$  content in leaves). Soluble sugars and starch content, specific

activity antioxidant enzymes – catalase, superoxide-dismutase, ascorbate-peroxidase, guaiacol-peroxidase – were monitored in roots and leaves by spectrophotometric methods (setup 3<sup>rd</sup>). For the determination of the expression levels of certain antioxidant isoenzymes (setup 3<sup>rd</sup>) in roots and leaves, RNA extraction was performed by phenol-chloroform-isoamyl alcohol method, and after several cleaning procedures, cDNA was synthesized, then with the aid of primer pairs designed in Primer3 software we used quantitative RT-PCR method (qTOWER, Analytik Jena, Germany).

Protein content and proteolytic activity of root apices were measured by photometric methods, electrolyte leakage was determined by a conductometer. For detecting DNA fragmentation, we performed agarose gel electrophoresis (setup 2<sup>nd</sup>).

We also measured the water potential of leaves by pressure chamber (setup 3<sup>rd</sup>), leaf pigment content by spectrophotometric method, CO<sub>2</sub> assimilation and stomatal conductance (setup 1<sup>st</sup> and 3<sup>rd</sup>) by a photosynthetic measuring system with infrared gas analyser (Li-6400, Li-Cor, Lincoln, NE, USA). Photosynthetic electron flow and the simultaneous activity of the photosystems (setup 1<sup>st</sup> and 3<sup>rd</sup>) were monitored by a chlorophyll *a* fluorescence and P700 analyser (DUAL-PAM-100, Heinz-Walz, Effeltrich, Germany).

Statistical analyses of our results were performed by Student's t-test or by analysis of variance followed by *post hoc* Duncan or Student-Newman-Keuls (SNK) tests.

## **Summary**

During our experiments, we investigated the ET sensitivity and the ET status-dependent salt stress responses of tomato plants using two different experimental designs. As a first approach, we investigated the effects of elevated ACC concentrations in the root zone of tomato plants on the most important physiological processes, which could possibly participate in the acclimation to a subsequent abiotic stress, as-an analogy for the inducible systemic resistance-mechanism. As a second approach, we examined the role of ET or ET

status in tomato plants during the early period of stress condition induced by salt treatments with different strength.

In accordance with our results, our conclusions are as follows:

1. **Exogenous ACC applied through the root zone of WT tomato plants induced significant ET emission from the tissues especially in the roots, but only above a concentration threshold value. However, exogenous ACC induces physiological changes below this threshold as well.**

2. **Small increases in root zone ACC concentrations (0.01-1.0  $\mu\text{M}$ ) enhanced dry biomass production in the shoots of WT tomato plants. Furthermore, the pattern of ROF/RNF generated by these treatments was unfavourable for the development of nitrosative stress, in plant root tips or leaf tissues.** In contrast to low concentrations, the presence of high exogenous ACC concentration (100  $\mu\text{M}$ ) in the root media induced a completely opposite response accompanied with enhanced ROF accumulation in the root apices and ROF/RNF accumulation in the leaves. In summary, exogenous ACC treatments induced enhanced  $\text{H}_2\text{O}_2$  accumulation and affected the patterns of NO and  $\text{ONOO}^-$  accumulation in concentration- or organ type dependent manner. Nevertheless, despite of the observed changes, the plants did not die even under high ACC concentration, furthermore, the weak oxidative stress can activate the antioxidant processes.

3. **The presence of exogenous ACC in the root zone could inhibit or stimulate photosynthesis and influence the activity of the photosystems in non-senescent tomato leaves in a concentration- and time dependent manner.** Lower concentrations of ACC (0.01 and 1.0  $\mu\text{M}$ ) enhanced the net  $\text{CO}_2$  assimilation ( $A_N$ ) after the 1<sup>st</sup> and 2<sup>nd</sup> days. **0.01  $\mu\text{M}$  ACC significantly enhanced photosystem I (PSI) quantum efficiency and altered its non-photochemical quenching profile**, although the impact of this concentration on PSII efficiency was small. Furthermore, treatment with the very high, 100  $\mu\text{M}$  ACC had a pronounced inhibitory effect on  $\text{CO}_2$  assimilation and PSII quantum efficiency, however, PSI quantum efficiency showed smaller sensitivity. **Photoprotective processes could be induced by all ACC concentrations with**

different kinetics and intensity, mostly through the enhancement of the PSI cyclic electron flow (CEF-PSI)-dependent non-photochemical quenching (NPQ).

4. **The small, but significant decrease in the  $K^+/Na^+$  ratio caused by 100  $\mu M$  ACC could be considered as weak salt stress, which might serve as a hardening effect in a putative subsequent osmotic/salt stress acclimation process. Thus, this could be defined as an ACC-induced eustress. 0.01-1.0  $\mu M$  ACC enhanced soluble sugar and sorbitol contents, which may contribute to the development of tolerance to an abiotic stress possessing an osmotic component.**

5. **The mutation of the ET receptor in *Nr* tomato plants resulted in enhanced susceptibility to supraoptimal salt concentrations. Root apical segments showed typical physiological symptoms of cell death even under sublethal stress, due to excess ROF and RNF accumulation in root tips caused by sublethal or lethal NaCl concentrations. In WT root tips, the accumulation of  $O_2^{\bullet-}$  occurred during lethal salt stress, and  $H_2O_2$  accumulated in the presence of sublethal salt concentration. In contrast to WT, *Nr* root apices blocked in ET signalling showed higher  $O_2^{\bullet-}/H_2O_2$  ratio even under 100 mM NaCl treatment, which is favourable for the induction of programmed cell death (PCD). Because of the detected ROF and RNF accumulation, the nitro-oxidative stress was more pronounced in *Nr* root apices even at 100 mM NaCl. This led to higher electrolyte leakage, enhanced DNA fragmentation, proteolysis and cysteine protease activity.**

6. Examining the role of ET in salt stress acclimation of plants with different ET status, it was concluded that the *Nr* mutation promoted ionic stress, which manifested in a decreased  $K^+/Na^+$  ratio, while exogenous ACC prevented the salt induced loss in leaf water potential, thus, lowered osmotic stress under salt stress.

7. **ET status of plants controls the accumulation of ROF and RNF molecules during the development of salt stress.** In root apices, both excess ET/ACC contents caused by exogenous ACC and the inhibition of ET signalling resulted in oxidative or nitro-oxidative stress under lethal salt stress, although the underlying mechanisms were different. Despite the observation, that the accumulation of  $O_2^{\bullet-}$  and  $ONOO^-$  was



enhanced at both conditions, this was higher in the case of ACC-treated WT root tips. While the cause of  $O_2^{\cdot-}$  accumulation in *Nr* roots was the inhibition of superoxide dismutase (SOD), the contribution of catalase (CAT) and – in the early hours – ascorbate peroxidase (APX) enzymes to the decomposition of  $H_2O_2$  were less intensive in the mutant than in ACC-treated roots. In summary, under lethal salt stress, the change of ET status (exogenous ACC, *Nr* mutation) in root tips enhanced salt sensitivity. In contrast to this, under tolerable salt stress, exogenous ACC alleviated the accumulation of  $O_2^{\cdot-}$  in the early hours, but not that of  $H_2O_2$ , which at the end, helped to mitigate oxidative stress. Early  $H_2O_2$  accumulation in root apices allows a faster induction of the expression and activity of antioxidant enzymes, as it can be seen in the case of *SIAPX2* or APX, respectively, while under lethal salt stress, the induction of CAT and guaiacol peroxidase (POD) specific activities contributed in  $H_2O_2$  decomposition at a higher extent, which at certain time points were more significant in ACC-treated or *Nr* roots. At the same time, despite the activation of antioxidant enzymes, the cell viability in root apices was significantly reduced in these samples due to lethal salt stress.

**8. The leaves showed lower sensitivity than the roots to salt stress within 24 hours. Comparing the tolerable and the cell death-inducing salt stress effects in the leaves, we could conclude that under the latter condition, much greater  $O_2^{\cdot-}$  accumulation was detected, which could be reduced by exogenous ACC pre-treatment or *Nr* mutation.** Similarly, higher  $H_2O_2$  levels could be observed at 250 mM NaCl concentrations, which was further enhanced by both ACC treatment or *Nr* mutation after 6 hours, thus, these tissues were exposed to severe oxidative stress. In shorter time interval, dramatic increase in NO or ONOO<sup>-</sup> accumulation could not be observed during the treatments. Under sublethal salt stress, elevated NO levels in ACC-treated or *Nr* mutant plants rather enhanced salt tolerance, while slight nitrosative stress could be developed due to greater ONOO<sup>-</sup> accumulation after 24 hours under lethal salt stress, which was alleviated by exogenous ACC.

The processes, which facilitate the formation  $O_2^{\cdot-}$ , such as photosynthetic electron transport or plasma membrane (PM)-bound NADPH oxidase, might participate in

developing high  $O_2^{\bullet-}$  levels. The rapid enhancement of SOD activity – in contrast to the roots – decreases  $O_2^{\bullet-}$  concentration under lethal salt stress after 24 hours. However, decreased  $O_2^{\bullet-}$  accumulation observed in ACC treated and the mutant leaves after 24 hours was paired with lower SOD specific activity compared to salt treated WT leaves, which indicates a decrease in  $O_2^{\bullet-}$  generating processes.

Under lethal salt stress, decreased APX and enhanced SOD specific activity contributed to the early accumulation of  $H_2O_2$  in ACC treated or *Nr* leaves. Later, in ACC treated or *Nr* leaves, neither CAT, POD nor APX could alleviate  $H_2O_2$  accumulation generated by increased SOD specific activity in ACC treated/*Nr* leaf samples. **Thus, the fine tuning in SOD and  $H_2O_2$  scavenging enzyme activity regulate  $H_2O_2$  content of leaves during lethal salt stress, which is highly depends on ET status of leaves.**

9. **ET status influences photosynthetic activity and sugar homeostasis in tomato plants under salt stress.** 100 mM NaCl added to root media decreased stomatal conductance rapidly in WT tomato leaves, this response was stronger under lethal salt stress, however, ACC treatment mitigated this salt induced effect in both cases. Net  $CO_2$  assimilation and  $C_i/C_a$  ratio were in good correlation with the changes in stomatal conductance under sublethal salt stress in all treatments, which showed that ET could control  $CO_2$  fixation mostly by the availability of  $CO_2$  in these samples. However, under lethal salt stress, besides stomatal factors, other processes could have been involved in the inhibition of  $CO_2$  assimilation, as it is confirmed by the increase in  $C_i/C_a$ . Interestingly, the decrease in  $A_N$  or the increase in  $C_i/C_a$  were significantly lower in the leaves of ACC treated or *Nr* plants under lethal salt stress, compared to WT plants. **Thus, ET participates in the development of salt stress responses as a function of stress intensity. The amount of the hormone or the impairment of its signalling caused contrasting effects during sublethal and lethal salt stress in  $CO_2$  assimilation.**

10. Salt treatments did not enhance photoinhibition in 24 hours, as it could be observed in  $F_v/F_m$ ,  $F_0$  and  $Y(NO)$  chlorophyll fluorescence parameters. Treatment with 100 mM NaCl did not affect PSII and PSI activity in the leaves of Ailsa Craig tomato cultivar. **However, in the presence of 100 mM NaCl, the  $Y(II)$  values of *Nr* mutants decreased**

**immediately, which is caused by higher, and more sensitive NPQ response in these plants.**

In good accordance with the reduction in Y(II) by lethal salt stress, the donor side limitation of PSI was enhanced with the simultaneous decrease in Y(NA) due to elevated CEF-PSI, which was further enhanced in the mutants during both salt stresses. Therefore, the enhanced, light regulated NPQ values under salt stress were induced by increased CEF-PSI in *Nr* mutants.

Interestingly, until the 6<sup>th</sup> hour of 250 mM NaCl treatment, exogenous ACC inhibited the induction of CEF-PSI, and therefore the induction of NPQ, which prevented the decrease of Y(II) or the consequent increase of Y(ND). This shows that, exogenous ACC delayed the decrease in PSII activity, but enhanced Y(NA), which governs the chance of a higher electron flow toward O<sub>2</sub>, O<sub>2</sub><sup>-</sup> formation and PSI photoinhibition. **Thus, ET could regulate net CO<sub>2</sub> assimilation through stomatal or non-stomatal factors, the quantum efficiency of the photosystems and photoprotective mechanisms, including PSI-CEF operation due to *Nr* receptor and the availability of ACC under salt stress. Nevertheless, PSI CEF could be suggested as an important and unknown participant in the process, during which ET represses the activation of violaxanthin-deepoxidase – key enzyme in xanthophyll cycle – which highly contributes to the greatest NPQ subfraction, the energy dependent quenching.**

11. Despite the lower CO<sub>2</sub> fixation activity, *Nr* mutant leaves possess significantly higher starch content than WT leaves, which could lead to the conclusion, **that ET signalling helps to maintain the balance between starch metabolism and photosynthesis.**

12. **The response of roots and leaves to the change in ET status was different.** Cell viability in root apices was decreased by salt stress, and both ACC-treated and *Nr* mutant root tips were more sensitive to sublethal salt exposure than WT. However, this did not necessarily increase mortality of plant individuals, because after a successful acclimation process in the shoot, newly formed adventitious roots could be induced. In contrast to *Nr* mutation, exogenous ACC enhanced stomatal conductance and net CO<sub>2</sub> assimilation in a short time interval and increased the quantum efficiency of PSII, therefore, it promoted

the adaptation of the shoot. **However, under lethal salt stress, *Nr* mutation or impaired ET signalling could induce positive changes in certain physiological processes, like more successful photoprotection and CO<sub>2</sub> assimilation. This indicates that under sublethal salt stress, both supraoptimal ET/ACC concentrations or the block in ET signalling decreases success of salt acclimation in the roots, but with different kinetics. It must be noted, that this does not necessarily lead to plant decay because of fine regulation of physiological processes. However, only *Nr* mutation affected photosynthesis negatively under sublethal salt stress, due to oversensitive photoprotection and decreased stomatal conductance. Our results also anticipate that in certain time points of stress development, the fine tuning of ET contents or signalling, or the alteration in the kinetics of ET production can help the salt acclimation process.**

### **Acknowledgement**

Our research was financially supported by OTKA K101243 and HUSRB/120/221/173 PLANTTRAIN IPA projects. The candidate's education was founded by the Doctoral School of Biology on the University of Szeged with state scholarship.

### **List of publications**

**MTMT ID: 10037573**

#### **The 2 mandatory publications for the doctoral procedure:**

- Borbély P., Bajkán Sz, Poór P, Tari I (2019) Exogenous 1-amiocyclopropane-1-carboxylic acid controls photosynthetic activity, accumulation of reactive oxygen or nitrogen species and macroelement content in tomato in long-term experiments. *Journal of Plant Growth Regulation*. 1-17. **IF: 2,179** (2018)
- Péter Poór, Judit Kovács, Péter Borbély, Zoltán Takács, Ágnes Szepesi, Irma Tari (2015) Salt stress-induced production of reactive oxygen- and nitrogen species and cell death in the ethylene receptor mutant *Never ripe* and wild type tomato roots *Plant Physiology and Biochemistry* 97: pp. 313-322. **IF: 2,756**

#### **Peer-reviewed publications:**

- Poór, Péter; Borbély Péter; Czékus, Zalán; Takács, Zoltán; Ördög, Attila; Popović, Boris; Tari, Irma (2019) Comparison of changes in water status and photosynthetic parameters in wild type and abscisic acid-deficient sitiens mutant of tomato (*Solanum lycopersicum* cv. Rheinlands Ruhm) exposed to sublethal and lethal salt stress *Journal of Plant Physiology* 232, pp. 130-140, 11 p. **IF: 2,825**
- Poór P, Borbély P., Bódi N, Bagyánszky M, Tari I (2019) Effect of salicylic acid on photosynthetic activity and chloroplast morphology under light and prolonged darkness. *Photosynthetica* 57, 367-376. **IF: 2,365**

- Zoltán Takács; Péter Poór; Péter Borbély; Zalán Czékus; Gabriella, Szalai; Irma Tari (2018) H<sub>2</sub>O<sub>2</sub> homeostasis in wild-type and ethylene-insensitive *Never ripe* tomato in response to salicylic acid treatment in normal photoperiod and in prolonged darkness Plant Physiology and Biochemistry, 126, pp. 74-85. **IF: 3,404**
- Poór P, Takács Z, Patyi G, Borbély P, Becsik O, Szekeres A, Tari I (2018) Dark-induced changes in the activity and the expression of tomato hexokinase genes depend on the leaf age. South African Journal of Botany, 118, 98-104. **IF: 1,504**
- Poór P, Ördög A, Czékus Z, Borbély P, Takács Z, Kovács J, Tari I (2018) Regulation of the key antioxidant enzymes by developmental processes and environmental stresses in the dark. Biologia Plantarum 62, pp 201–210. **IF: 1,384**
- Poór P, Borbély P, Kovács J, Papp A, Szepesi Á, Takács Z, Tari I (2014) Opposite extremes in ethylene/nitric oxide ratio induce cell death in cell suspension culture and in root apices of tomato exposed to salt stress. Acta Biologica Hungarica 65: pp. 428-438. **IF: 0,589**

**Cumulative IF: 17,007**

### Other scientific publications:

- Orbán Cs., Csajbók Cs., É. Hegedűs N., Borbély P. (2015): Alteration of peroxidase activity, chlorophyll content and antioxidant-capacity of corn salad (*Valerianella locusta*) during storage. BioTechnology: An Indian Journal. 11(2):66-70.

### Conference presentations/posters related to Ph.D. dissertation:

- Borbély Péter; Poór Péter; Hegedűs Dóra; Tari Irma (2019) Oxidatív stresszválasz kialakulása különböző etilén státuszú paradicsomban sóstressz alatt In: Poór Péter; Blázovics Anna (eds.) Magyar Szabadgyök-Kutató Társaság X. Kongresszusa: Program és összefoglalók Szeged, Hungary, University of Szeged, (August 2019) p. 26 (**presentation**)
- Borbély Péter, Poór Péter, Tari Irma (2018) Az etilén prekursor, 1-aminociklopropán-1-karbonsav hatása paradicsomnövények fotoszintetikus aktivitására Hazai Fotoszintézis-kutatók Találkozója November 2018. Mátrafüred, Hungary (**presentation**)
- Borbély P, Czékus Z, Hegedűs D, Kurtulus G, Péter P, Tari I. (2017) Az etilén szerepe a reaktív oxigén- és nitrogénformák akkumulációjának szabályozásában sóstressznek kitett paradicsomnövényekben. A Magyar Szabadgyök-Kutató Társaság 9. Kongresszusa, August 2017., Gödöllő, Hungary Absztraktgyűjtemény p 25. (**presentation**)
- Péter Borbély, Zoltán Takács, Orsolya Csíkos, Péter Poór, Irma Tari (2017) Exogenous ACC treatment affects photosynthetic activity and related parameters of tomato plants by a concentration dependent manner. A Magyar Növénybiológiai Társaság 12. kongresszusa, August 2017., Szeged, Hungary (**poster**)
- Péter Borbély, Péter Poór, Gábor Patyi, Irma Tari (2015) Effect of Ethylene Precursor ACC Pre-Treatment on Photosynthesis Under Salt Stress In: Jian-kang Zhu, Alisher Touraev (eds.) Plant Abiotic Stress Tolerance III: Programme and Abstracts. June 2015., Vienna, Austria. 63 (**poster**)

### Other conference presentations/posters

- Marschall Marianna, Borbély Péter (2018) Újranedvesedés alatti fényvédelmi és regenerációs mechanizmusok háttér folyamatainak, komponenseinek vizsgálata kiszáradástűrő és kiszáradásérzékeny mohafajokban. Hazai Fotoszintézis-kutatók Találkozója November 2018., Mátrafüred, Hungary (**presentation**)
- Marschall, M; Borbély, P; Prné-Kónya, E; Sütő, Sz: Background processes and the components of photoprotection and regeneration under rehydration in desiccation-tolerant and desiccation-sensitive bryophytes Paper: 29, 1 p. In: Plant Biology Europe 2018 Conference : Photosynthesis Diversity Copenhagen, Denmark (2018) p. 1 (**poster**)
- Zalán, Czékus; Orsolya, Csíkos; Dóra, Hegedűs ; Péter, Borbély ; Attila, Ördög ; Péter, Poór: Investigation of dark modulated endoplasmatic reticulum (ER) stress in tomato plants p. 116 In: Tamás, László; Zelenyánszki, Helga (eds.) Fialat Biotechnológusok Országos Konferenciája "FIBOK 2018": Abstract Book, Szeged, Hungary, (2018) (**presentation**)

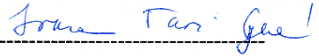
- Poór Péter, Czékus Zalán, Borbély Péter, Takács Zoltán, Tari Irma: Növényi antioxidáns enzimek szalicilsav kezelést követő etilénfüggő szabályozása sötétben In: Mézes Miklós (eds.) Magyar Szabadgyök-Kutató Társaság IX. Kongresszusa és az MTA ÉKB Mikroelem Munkabizottságának Tudományos Ülése. August 2017 Gödöllő, Magyarország. (**presentation**)
- Marschall M, Borbély P., Sütő Sz (2017) Újránvedesés alatti fényvédelmi és regenerációs mechanizmusok háttérfolyamatainak, komponenseinek vizsgálata kiszáradástűrő és kiszáradásérzékeny mohafajokban In: Györgyey János (eds.) A Magyar Növénybiológiai Társaság XII. Kongresszusa. 72 p. August 2017. Szeged, Hungary. (**presentation**)
- Kovács J, Poór P., Borbély P., Czékus Z, Tari I (2017) Sóstresszre adott válaszreakciók paradicsomban: nitrogénmonoxid, reaktív oxigénformák és proteolízis indukciója abszcizinsav hiányos paradicsom mutánsokban. A Magyar Szabadgyök-Kutató Társaság 9. Kongresszusa, August 2017., Gödöllő, Absztraktgyűjtemény 24. old. (**presentation**)
- Poór Péter; Zoltán, Takács ; Péter, Borbély ; Zalán, Czékus ; Irma, Tari (2017) Ethylene dependent changes in hydrogen-peroxide homeostasis after salicylic acid treatment in tomato p. 21 In: Andreas, Bachmair; Alisher, Touraev (eds.) International Conference Plant Molecular Physiology:Programme and Abstracts February (2017) (**poster**)
- Poór Péter, Judit Kovács, Ágnes Szepesi, Péter Borbély, Gábor Patyi, Irma Tari (2016) Salt stress-induced oxidative stress in ethylene signaling mutant, Never ripe tomato. HUSBR/1203/221/173 „PLANTTRAIN”: Joint development of higher education and training programmes in plant biology in support of knowledge-based society. Closing Conference. May 2016., Novi Sad, Serbia. (**presentation**)
- Zoltán Takács, Zalán Czékus, Péter Poór, Péter Borbély, Irma Tari (2016) Effect of light on the salicylic-induced oxidative stress in tomato. HUSBR/1203/221/173 „PLANTTRAIN”: Joint development of higher education and training programmes in plant biology in support of knowledgebased society. Closing Conference. May 2016., Novi Sad, Serbia (**presentation**)
- Péter Poór, Zoltán Takács, Péter Borbély, Zalán Czékus, Gábor Patyi, Irma Tari (2016) Involvement of ethylene in hydrogenperoxide metabolism in the leaves of salicylic acid treated tomato. Plant Biology Europe EPSO/FESPB 2016 Congress. June 2016., Prague, Czech Republic (**poster**)
- Péter Poór, Zalán Czékus, Gábor Patyi, Péter Borbély, Judit Kovács, Zoltán Takács, Irma Tari: Investigation of Salt Stress-induced Changes in Water Status, Photosynthetic Parameters and Cysteine Protease Activity in Wild Type and Abscisic Acid-Deficient Sitiens Mutant of Tomato (*Solanum Lycopersicum* cv. Rheinland Ruhm). In: Andreas Bachmair, Klaus Palme, Alisher Touraev (eds.) Programme and Abstracts: Plant Model Species: Fundamentals and Applications. February 2016., Vienna, Austria. p.23. (**poster**)
- Tari Irma, Borbély Péter, Csizsár Jolán, Horváth Edit, Poór Péter, Szepesi Ágnes, Takács Zoltán (2016) Szalicilsav kémiai edzés hatása a paradicsom sóstressz toleranciájára In: Rajnai Zoltán, Fregán Beatrix , Marosné Kuna Zsuzsanna (eds.) Book of abstracts. 1-2. kötet. 1159 p. Budapest, Hungary, May 2016., pp. 407-416. (ISBN:978-615-5460-97-5) (**presentation** & assay)
- Poór, P., Kovács, J., Borbély, P., Takács, Z., Szepesi, Á., Tari, I. (2015) Sóstressz indukált változások a reaktív oxigén és nitrogénformák akkumulációjában etilénreceptor mutáns *Never ripe* és vad típusú paradicsomban. A Magyar Szabadgyök-Kutató Társaság VIII. Kongresszusa, November 2015., Budapest, Hungary Absztraktfüzet, pp. 32.
- Péter Poór, Attila Ördög , Barnabás Wodala , Péter Borbély , Ionel Samfira , Monica Butnariu , Dóra Hegedűs , Katalin Szabó , Attila Pécsváradai , Irma Tari (2015) Effect of Salinity Stress on Ion Accumulation and on the Photosynthetic Activity of a New Energy Plant, *Phalaris arundinacea* Cultivars. In: Alapi Tünde, Ilisz István (eds.) Proceedings of the 21st International Symposium on Analytical and Environmental Problems. 445 p. Konferencia helye, ideje: Szeged, Magyarország, Septemeber 2015., Szeged 2015. p. 392-4. (ISBN:978-963-306-411-5) (**poster** és kiadvány)
- Péter Poór, Zoltán Takács, Péter Borbély, Ágnes Szepesi, Irma Tari (2015) Light and Darkness Modulate the Oxidative Burst And Enzymatic Antioxidant Systems In Salicylic Acid-Treated Tomato Leaf In: Laura De Gara, Massimo Delledonne (eds.) 12<sup>th</sup> International Conference on Reactive Oxygen and Nitrogen Species in Plants: from model systems to field.. Verona, Italy, 2015.06.24-2015.06.26.p. 111. (**poster**)
- Ágnes Szepesi, Péter Borbély, Ágnes Hurton, Zoltán Takács, Szabolcs Tóth, Izabella Kovács, Christian Lindermayr, Irma Tari (2015) Polyamine catabolism under salt stress: inhibiting diamine oxidase by aminoguanidine. In: Irma Tari, Dániel Benyó Joint development of higher education and training

- programmes in plant biology in support of knowledge-based society: Opening Conference, BOOK OF ABSTRACTS. April 2015., Szeged, Hungary, p. 12. 1 p. (**presentation**)
- Tari Irma , Borbély Péter , Csiszár Jolán , Gémes Katalin , Horváth Edit , Kovács Judit , Poór Péter, Szepesi Ágnes, Takács Zoltán (2014) Sóstressz tolerancia fokozása szalicilsavval paradicsomban: az abszcizinsav szerepe. In: Fodor F (eds.) Paál Árpádtól a molekuláris növénybiológiáig: Tudományos ülés Paál Árpád születésének 125. és intézetigazgatói kinevezésének 85. évfordulója alkalmából. December, 2014., Budapest, Magyarország, pp. 55-59. (ISBN:978-963-284-561-6) (**presentation** és kiadvány)
- Poór Péter, Kovács Judit, Borbély Péter Gábor, Takács Zoltán, Szepesi Ágnes, Tari Irma (2015) Exogén NO hatása a sóstressz indukált fiziológiai válaszreakciókra paradicsomban. Magyar Tudomány Ünnepe, Az MTA SZAB Biológiai Szakbizottság ünnepi tudományos ülése, Reprezentatív előadások a biológiai munkabizottságok kutatási területeiről. November 2014. Szeged, Hungary. (**presentation**)
- Péter Borbély, Péter Poór, Judit Kovács, Zoltán Takács, Gábor Patyi, Ágnes Szepesi, Irma Tari (2015) Exogenous sodium nitroprusside alleviates salt-induced changes in photosynthesis of tomato leaves. In: Györgyey J (eds.): 11th Congress of the Hungarian Society of Plant Biology: Book of Abstracts.: September 2014., Szeged, Hungary, p. 61. (**poster**)

## Conflict of interest

I, myself as corresponding author or first author of the following publications declare that authors have no conflict of interest and Péter Gábor Borbély Ph.D. candidate had a great contribution to the published results. Results discussed in his thesis are regarded as outcomes of his own scientific work.

Borbély P, Bajkán Sz, Poór P, Tari I (2019) Exogenous 1-amiocyclopropane-1-carboxylic acid controls photosynthetic activity, accumulation of reactive oxygen or nitrogen species and macroelement content in tomato in long-term experiments. *Journal of Plant Growth Regulation*. 1-17.  
Szeged, 23. September 2019.

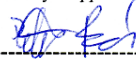


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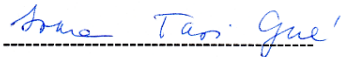
Péter Poór, Judit Kovács, Péter Borbély, Zoltán Takács, Ágnes Szepesi, Irma Tari (2015) Salt stress-induced production of reactive oxygen- and nitrogen species and cell death in the ethylene receptor mutant *Never ripe* and wild type tomato roots *Plant Physiology and Biochemistry* 97:pp. 313-322.  
Szeged, 23. September 2019.



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