

Ph.D. Thesis

**Comparative analysis of the effect of exogenous SA on light and dark in wild-type and ethylene receptor mutant, *Never ripe* tomato plants**

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2018

Szeged

## **INTRODUCTION**

Biotic stresses is caused in plants due to damage instigated by other organisms, like insects, disease (fungal, bacterial, and viral), which are major limitations to crop yield. The cellular response to biotic stress is an oxidative and nitrosative burst involving production of reactive oxygen species (ROS) and nitric oxide (NO). Salicylic acid (SA) is a natural phenolic compound, which accumulates under biotic stress and controls physiological and biochemical functions in plants. SA plays an important role in oxidative and nitrosative stress by modulating the activity of some antioxidant enzymes. Polyamines (PAs) are low molecular weight organic compounds acting as signal molecules by directly or indirectly involved in the biotic stress response pathway. The metabolism of PAs is regulated not just by SA but also by the gaseous phytohormone ethylene (ET), which is a key regulator in plant growth and developmental process as well as biotic stress response. Furthermore, ET and PAs may be an antagonistic relationship because they share a common biosynthetic precursor. However, plant immune defence also depends on the environmental factors such as light. Excess of light energy under stress conditions leads to oxidative stress, which may contribute to the initiation of cell death in tissues.

## AIMS OF THE WORK

The aim of our work was to study the effects of the sublethal (0.1 mM) and lethal (1 mM) concentrations of SA in tomato leaves during normal photoperiod and prolonged darkness. The changes in biochemical, physiological and molecular processes are determined upon treatment of hydroponically grown tomato with sublethal and lethal concentrations of SA. However, in plants, the potential the relationship between PAs and ET in the biotic stress has so far not been examined in detail. So in order to further address the known interaction between these components, we have used the ethylene-insensitive *Never ripe (Nr)* tomato (*Solanum lycopersicum* L.) mutant, which blocks ethylene responses, after sublethal and lethal SA treatment in the presence or absence of light.

Specifically, these aims are:

1. How sublethal and lethal SA treatments affect the endogen SA content, membrane integrity and malondialdehyde (MDA) content, a biochemical marker of lipid peroxidation in the wild type tomato leaves during normal photoperiod or prolonged darkness?
2. How do the activity and gene expression of PA metabolism enzymes and the free PAs content change after the sublethal and lethal SA treatment in the presence or absence of light. Can PA metabolism regulate the acclimatitition or cell death induction?
3. While it is well established that SA and PA catabolic pathway can induce H<sub>2</sub>O<sub>2</sub> content, which has been found to play an important role in oxidative stress-related mechanisms, our experiments focused on O<sub>2</sub><sup>-</sup>, H<sub>2</sub>O<sub>2</sub>, NO content, furthermore the activity and expression of antioxidant enzymes during SA treatments in light or darkness. Can metabolism of PAs, especially catabolism of them and/or activity of antioxidant enzymes contribute to the H<sub>2</sub>O<sub>2</sub> content during SA treatment? What are the differences in these components during normal photopriod and prolonged darkness?
4. How do the sublethal and lethal SA treatments affect H<sub>2</sub>O<sub>2</sub> content in the leaves of ethylene receptor mutant, *Never ripe (Nr)* in light and dark?

5. How can both SA treatments affect on content of SA-, ET- and free PAs, and the activity and gene expression of enzymes involved in PAs metabolism in the leaves of ET receptor mutant tomato plants under the two types of light conditions?
6. How does the absence of ET signalling influence on the activity and gene expression of the antioxidant enzymes after sublethal and lethal SA treatments? What are the differences during light and darkness?
7. Can ET signalling contribute to the SA-induced mechanisms through the activation of PAs metabolism and antioxidants enzymes?

## **MATERIALS AND METHODS**

- **Plant materials and growth conditions**

Wild-type (*Solanum lycopersicum* Mill. L. cvar. Ailsa Craig) and ethylene receptor mutant *Never ripe* tomato plants were grown in hydroponics, under controlled conditions in the greenhouse. 8 weeks old tomato plants were treated with 0.1 mM or 1 mM SA supplied in the nutrient solution. Half of the plants remained for 24 h under the growing light/dark cycle (light samples) or half of them were put into prolonged darkness (dark samples). The samples were prepared from the second, fully expanded young leaves at least in 3 replicates in case of WT 1, 3, 6, 12, 24 h and in case of *Nr* 24 h after the different SA treatments.

- Salicylic acid extraction and measuring by HPLC
- Determination of electrolyte leakage by conductivity meter
- Determination of malondialdehyde content
- Measurement of free polyamine levels by HPLC
- RNA isolation, DNase treatment, cDNA qRT-PCR
- Determination of terminal diamine- and polyamine oxidase activities
- Histochemical detection of superoxide production
- Measurement of the H<sub>2</sub>O<sub>2</sub> content by spectrophotometer and histochemical, respectively
- Detection of NO production by fluorescence microscopy
- Measurement the ethylene production by gas chromatography
- Determination of antioxidant enzyme activities by spectrophotometer
- Superoxide dismutase enzyme
- Catalase enzyme
- Ascorbate peroxidase enzyme

- Guaiacol peroxidase enzyme
- Native PAGE analysis of NADPH oxidase and antioxidant enzyme activities
- Determination of protein content

After analyses of variance (ANOVA) a multiple comparison followed by Duncan test was performed with SigmaPlot version 12 software.

## RESULTS

The aim of our work was to study the effects of normal photoperiod or prolonged darkness on common features or differences of oxidative stress induced by sublethal or lethal concentrations of salicylic acid (SA) in the leaves of tomato (*Solanum lycopersicum* cv. Ailsa Craig). Furthermore, the time- and concentration-specific induction of defence signaling was investigated in the leaves of wild type (WT) and ethylene (ET) insensitive *Never ripe* (*Nr*) mutants. Our work focused on ET-dependent effects of sublethal (0.1 mM) and lethal (1 mM) SA treatments under light and dark conditions on various components of oxidative stress and polyamine (PA) metabolism. Furthermore, ET receptor *Nr* mutants of tomato make it possible to analyse the role of ET signaling and the functions of ET in SA-induced H<sub>2</sub>O<sub>2</sub> metabolism.

Our results can be summarized as follows:

1. In the present study, we demonstrated that sublethal and lethal SA treatments could affect H<sub>2</sub>O<sub>2</sub> metabolism differently in the presence or absence of light in tomato leaves. Our results confirmed the observation that H<sub>2</sub>O<sub>2</sub> accumulation of young leaf tissues was stimulated in the light by SA, but it was delayed and the maximum was lower in the prolonged dark period. Moreover, 1 mM SA induced higher H<sub>2</sub>O<sub>2</sub> levels in the illuminated leaves than 0.1 mM SA and in these leaves two peaks of H<sub>2</sub>O<sub>2</sub> were detected, which cannot be observed in the plants kept under prolonged darkness. The lack of the first, priming burst of H<sub>2</sub>O<sub>2</sub> in the dark at 1 mM SA suggests that the early source of H<sub>2</sub>O<sub>2</sub> depends on the presence of light.
2. SA has a concentration- and light dependent effects on membrane integrity, electrolyte leakage and cell death induction. SA treatments induced not only H<sub>2</sub>O<sub>2</sub> accumulation but also the production of NO in a light- and concentration dependent manner. These results suggest that high SA concentration effectively induced H<sub>2</sub>O<sub>2</sub> and NO accumulation eliciting simultaneous oxidative- and nitrosative stress and concomitant cell death in the illuminated leaves. In the dark, leaf tissues produced less H<sub>2</sub>O<sub>2</sub> and NO, which remained below the control level, the tissues were exposed to moderated stress than in the light, which

slowed down the initiation of cell death program. In contrast, the treatment with 0.1 mM SA generated oxidative stress without nitrosative stress and induced an acclimation process during normal photoperiod or prolonged darkness in WT plants.

3. The relative importance of arginine decarboxylase (ADC) and ornithine decarboxylase (ODC) activities in putrescine (Put) biosynthesis was different at low and high SA because *ODC* gene has not been induced by 0.1 mM SA. However, *ODC* was highly up-regulated by high concentration of SA suggesting that ADC is more important in Put biosynthesis during stress acclimation than ODC. It can be concluded that much higher induction occurred after lethal SA treatment in *SIADC*, *SIODC* and spermine synthase (*SISPMS*) expression than after sublethal one, but the expression of spermidine synthase (*SISPDS*) has not been changed significantly with increasing SA concentrations. The expression pattern of the PA biosynthetic genes correlated well with the PAs accumulation. Thus, it can be concluded that PA biosynthesis exerts a significant control over PA level in the first 24 h of SA treatment.
4. 0.1 mM SA induced DAO activity and the expression of *SIDAO1* and *SIDAO2* both in the light and dark, nevertheless 1 mM SA caused much lower induction and significant changes occurred only in the dark and not in the light. The expression of *SIPAO1* at both SA concentrations was significantly higher in the dark after 6 h than in control plants but this was not correlated with the terminal oxidation of higher PAs. Moreover, we did not find strict temporal coincidence between H<sub>2</sub>O<sub>2</sub> accumulation and PA catabolism. This means that ROS production by other processes at 1 mM SA can overrun ROS generated by terminal oxidation of PAs in actively photosynthesizing tissues.
5. The NADPH oxidase activity, which is responsible for the fast accumulation of superoxide anion radical, was induced by 1 mM SA within an hour under normal photoperiod. The expression of the chloroplastic superoxide dismutase (*Cu/Zn-SOD*) and mitochondrial *Mn-SOD* coding genes were increased by 1 mM SA treatment in the light samples while there were no major changes at 0.1 mM SA. These suggest that the oxidative stress may activate the expression of chloroplastic *Cu/Zn-SOD* and mitochondrial *Mn-SOD*. However, the enzyme activities correlated only slightly with the changes in gene expression. Interestingly, both SA treatments inhibited the activity of catalase (CAT)

enzyme, which was independent of the illumination. The other H<sub>2</sub>O<sub>2</sub> scavenging enzyme, ascorbate peroxidase (APX) exhibited the highest light-dependency after SA treatments. In the first hours APX activity was inhibited by 1 mM SA, which can contribute in parallel with the inhibition of CAT activity to the first peak of H<sub>2</sub>O<sub>2</sub> accumulation. In contrast to APX, guaiacol peroxidase (POD) activity increased upon 1 mM SA treatment later under both environments. Thus, POD activity can contribute to the decomposition of H<sub>2</sub>O<sub>2</sub> in the dark, which is particularly important in the absence of CAT and APX activity in SA-mediated protective actions.

6. SA-induced increases in H<sub>2</sub>O<sub>2</sub> were also observed in *Nr* plants. The most interesting tendencies could be detected at 1 mM SA concentration. While the inhibition of ET signalling by the *Nr* mutation decreased the SA-induced H<sub>2</sub>O<sub>2</sub> content, EL and necrotic lesions on the leaves in the light compared to WT, but it resulted in pronounced H<sub>2</sub>O<sub>2</sub> accumulation, increased EL and higher necrotic lesions under prolonged darkness. This suggests that not only SA and ET levels but also their signalling pathways are dependent on the presence or absence of light. This suggests that the *Nr* mutants were more tolerant to SA-induced oxidative stress than WT in normal photoperiod but they proved to be more sensitive during prolonged darkness.
7. Exogenous application of SA had a concentration dependent impact on PAs contents in WT under light and dark conditions, which was most pronounced for spermine (Spm) content in 1 mM SA treatment under light and for Put concentration in 1 mM SA treatment under dark condition. On the other hand, PAs concentration was higher in WT compared to *Nr* after both SA treatments under light and dark conditions. The lack of active ET signalling could decrease free PAs content by the inhibition of the expression of PA biosynthetic genes, which was most pronounced in case of *SISPMS*. Furthermore, decreased PA contents may contribute to SA-induced cell death in the leaves of *Nr* plants.
8. *Nr* leaf exhibited almost always higher DAO and PAO activities compared with WT even in control conditions. If *Nr* plants were treated with 1 mM SA, DAO activity increased and PAO activity decreased under normal photoperiod, but under darkness, activity of both enzymes increased significantly compared to *Nr* control. In our experiments DAO and PAO activity showed strict correlation with PAs content. The increased activities of terminal catabolic enzyme may play a



role in increased inter-/intracellular levels of ROS ( $\text{H}_2\text{O}_2$  and  $\cdot\text{O}_2^-$ ) under darkness in the *Nr* leaves.

9. The  $\text{H}_2\text{O}_2$  accumulation in WT leaves in response to 1 mM SA treatment is mainly determined by increased SOD and decreased CAT activities in the light, thus APX and POD proved to be main participants in  $\text{H}_2\text{O}_2$  scavenging. In contrast, in a prolonged dark period the SOD activity and the expression of *S1Cu/ZnSOD* gene were activated in *Nr* mutants exposed to 1 mM SA but the absence of APX and POD activation led to a significant accumulation of  $\text{H}_2\text{O}_2$  in these samples. These results suggest that the SA-induced  $\text{H}_2\text{O}_2$  metabolism is regulated by different enzymes in WT and ET signalling mutant plants, which is modified by the presence or absence of light.

## PUBLICATION LIST

*Author ID: 10039049*

### *Full papers*

*(Thesis is based on articles marked by \*)*

- \* **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* (IF: 2.724)
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