

Ph.D. Thesis

**Investigation of salt stress- and salicylic acid induced
physiological changes in tomato plants:
acclimation or programmed cell death**

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INTRODUCTION

Programmed cell death (PCD) is genetically defined process which plays an important role during the normal life cycle of plants and in response to changing environments. PCD also plays a role in the plant defense mechanisms. It can be triggered by developmental processes (e.g. leaf morphogenesis, senescence) and by abiotic or biotic stressors (e.g. pathogen attack, hypersensitive response (HR)). PCD is associated with special morphological and biochemical changes both in animal and plant systems, but the differences between plant and animal PCD mechanisms have not yet been discussed in detail.

PCD induced by various abiotic factors such as salt stress may negatively affect the biomass production of many crop plants and may cause serious yield loss in the agriculture. Supraoptimal salt concentrations usually cause osmotic-, ionic - and oxidative stress and due to them may induce PCD in plant cells.

Salicylic acid (SA) is a key molecule in the induction of HR which has been evolved as a defense reaction against biotrophic pathogens or in systemic acquired resistance. SA can also cause changes in the water status of plants and can result in cell death-inducing oxidative stress. In earlier works it was shown that the sublethal concentrations of SA applied in hydroponic culture through the root system generated pre-adaptation responses which led to salinity tolerance.

AIMS OF THE WORK

The aim of our work is to study the effects of the lethal concentrations of NaCl and SA on the cell death initiation in tomato plants in order to highlight the common features and differences in the NaCl- and SA-induced PCD. The changes in biochemical, physiological and molecular processes are determined upon treatment of hydroponically grown tomato with sub-lethal and lethal concentrations of NaCl or SA. Specifically, these aims are:

1. What is the limit between sub-lethal and lethal SA and NaCl concentrations which can improve stress acclimation in tomato or can induce PCD? What is the physiological background of PCD induction?
2. How do SA and NaCl treatments affect stomatal conductance, photosynthetic activity and chlorophyll *a* fluorescence parameters in the leaves? What is the effect of decreased photosynthetic activity on PCD induction during treatments with lethal concentrations of SA or NaCl?
3. Since the CO₂ diffusion and thus CO₂ fixation rate can be controlled by stomata closure, our experiments were focused on if SA has direct control over stomatal movement in abaxial epidermal peels? What is the role of reactive oxygen species (ROS among others H₂O₂) and nitric oxide (NO) in SA-induced signalling in guard cells?
4. Can SA treatments directly affect the photosynthetic performance and chlorophyll *a* fluorescence induction parameters of guard cells (Fv/Fm, Yield, qP, NPQ, Rel. ETR)? How does guard cell photosynthesis determine stomatal movement?
5. What are the common features and differences in the SA- and NaCl-induced PCD mechanisms concerning the ethylene (ET) production, ion homeostasis, ROS- and NO production of tissues? What kind of “proapoptotic” (cysteine proteases, metacaspases, vacuolar processing enzymes, MAPKs) and “antiapoptotic” (Bax Inhibitor 1, PR) genes are activated or can be involved in the initiation or prevention of cell death program?
6. How do the total protease activity and the activity of specific proteases separated by gelatin-SDS-PAGE change after the SA- and NaCl treatment?
7. Which are the common features and differences in the signalling intermediates of NaCl- and SA- induced cell death in tomato cell suspension culture? What kind of

cytomorphological changes can be observed during the SA- and NaCl-induced PCD?

8. Is the cell suspension culture a good model of the root meristem cells?

MATERIALS AND METHODS

1. Experiments with intact plants

- Plant material and the applied treatments

Tomato plants (*Solanum lycopersicum* Mill. L. cvar. Rio Fuego) were grown in hydroponics, under controlled condition in the greenhouse. Plants were treated with 10^{-7} - 10^{-2} M SA or 100-250 mM NaCl in the culture solution for 6 or 24 hours.

- Measurement of H₂O₂ content by spectrophotometer
- Detection of superoxide accumulation
- Measurement of stomatal conductance by steady-state porometer
- Measurement of photosynthetic light and CO₂ response curves, chlorophyll a fluorescence by portable photosynthesis system
- Measurement of pigment and total sugar content by spectrophotometer
- Measurement of ET production by gas chromatography
- Detection of viability, ROS- and NO production by fluorescence microscopy
- *In silico methods*: homology tree based on protein sequences (Sol Genomics Network, ClustalW, Dendroscope) primer pair design (NCBI, Primer3), promoter analysis (PlantCARE)
- RNA isolation, DNase treatment, cDNA, qRT-PCR
- Determination of macroelements in leaf and root tissues by atomic absorption spectrometry (AAS)
- Determination of protein content and protease activity by spectrophotometer and by gelatin-SDS-PAGE, respectively
- Measurement of electrolyte leakage by conductivity meter
- Detection of DNA fragmentation on agarose gel

2. Experiments with guard cells

- Preparation and incubation of epidermal strips

Epidermal peels were manually detached from the abaxial surface of the second, fully expanded young, non-treated tomato leaves. The strips were transferred to dishes containing opening buffer. After 3 h of the incubation, the epidermal strips were treated with 10^{-7} - 10^{-3} M SA in the same opening buffer for another 3 h under the same conditions.

- Detection of viability, ROS- and NO production by fluorescence microscopy
- Measurement of photosynthetic performance of guard cells pairs by microscopy-pulse amplitude modulation chlorophyll fluorometer
- Determination of the effects of different modulators (inhibitors and scavengers) on SA-induced stomatal movement

3. Experiments with tomato suspension cultures

- Callus induction
- Suspension culture preparation

Suspension cultures were treated with 100-250 mM NaCl or 10^{-4} - 10^{-3} M SA (pH 5.8).

- Cell growth and pH determination
- Determination of macroelement contents of the cells by AAS
- Measurement of electrolyte leakage by conductivity meter
- Measurement of ET production by gas chromatography
- Detection of viability, ROS- and NO production by fluorescence microscopy
- Cell death determination with TUNEL-assay
- Detection of DNA fragmentation on agarose gel
- Determination of the signalling components of NaCl- and SA-induced PCD by microscopy

RESULTS

Programmed cell death (PCD) is an integral part of the plant development and in the response to changing environments. PCD is induced by various abiotic stressors such as high salinity. A special type of PCD in plants is the hypersensitive response during biotic stress which is mediated by salicylic acid (SA). Salt stress results in the disturbance in ion homeostasis, water status and redox equilibrium of plant cells. SA can also cause changes in the water status of plants and can result in oxidative stress but it is not known how SA affects the ion homeostasis of cells. The aims of our work were to study the effects of different concentrations of NaCl and SA on the cell death initiation in tomato in order to highlight the common features or differences in the NaCl- and SA-induced PCD.

Our results can be summarized as follows:

1. Supraoptimal concentrations of NaCl and SA increased the amount of reactive oxygen species (ROS) and H₂O₂ content of leaf tissues and root apices. In parallel, the viability of plants treated with 250 mM NaCl and 10⁻³-10⁻² M SA decreased significantly. The DNA in the root tissues were fragmented after treatment with 10⁻² M SA and 250 mM NaCl after 24h. In contrast, the treatment with 100 mM NaCl and 10⁻⁴ M SA generated oxidative stress and induced acclimation process in plants.
2. Supraoptimal concentrations of NaCl and SA increased the amount of ROS and H₂O₂ content of leaf tissues in the light. The inhibition of photosynthetic electron transport can significantly contribute to the generation of ROS in chloroplasts. The photosynthetic performance can be controlled by the limitation of CO₂ diffusion through stomatal pores. The addition of NaCl at 100-250 mM and SA at 10⁻⁷-10⁻² M to the hydroponic culture of tomato plants for 6 hours resulted in stomatal closure on intact leaves. In parallel with

stomatal closure 100-250 mM NaCl and 10^{-3} - 10^{-2} M SA decreased the maximal CO₂ fixation rate (A_{max}), and the initial slopes of the CO₂ (A/C_i) and light response ($A/PPFD$) curves, the carboxylation efficiency (CE) and the photosynthetic quantum efficiency (Q), respectively and relative electron transport rate (Rel. ETR) in intact leaves. Those concentrations of SA which decreased the photosynthetic performance in intact leaves led later to PCD.

3. Salicylic acid (SA) has direct control over stomatal movement by increasing the levels of ROS and nitric oxide (NO) and by changing the photosynthetic activity of guard cells (GC). 10^{-7} and 10^{-3} M SA induced stomatal closure on the abaxial epidermal peels of tomato leaf but stomata remained open at 10^{-4} M. At those concentrations which reduced stomatal aperture ROS and NO were raised. The accumulation of active oxygen and nitrogen forms could be prevented by specific scavengers which were effective inhibitors of stomatal closure by SA. In contrast to other plant species, GCs did not show a long-lasting accumulation of ROS in the presence of 10^{-4} M SA and their NO content declined below the control level which led to stomatal opening.
4. Increasing SA concentrations resulted in a significant decrease in maximum and effective quantum yield of PSII photochemistry as well as in the photochemical quenching parameter of GCs. In the presence of 10^{-7} and 10^{-4} M SA, chloroplasts of GCs sustained a higher maximum relative electron transport rate than in the presence of 10^{-3} M, suggesting that SA induced inhibition of the GC photosynthesis can affect stomatal closure at high SA concentrations.
5. The lethal concentration of SA (10^{-3} - 10^{-2} M) and NaCl (250 mM) decreased the ethylene (ET) production in the roots while ET emission was induced by sublethal concentration of NaCl (100 mM). The sublethal concentration of SA did not cause any change in ET level. Treatments with supraoptimal concentration of NaCl and SA increased the ROS and NO production in the root apices of tomato plants, which led to significant loss of tissue vitality.
6. The specific genes involved in cell death program were induced by NaCl and SA and their expression levels were analyzed by RT-PCR. The expression of *SIB1* coding for the antiapoptotic Bax Inhibitor increased significantly in the leaves treated with 10^{-2} M SA, but decreased in the root treated with lethal concentrations of SA and NaCl. In parallel, the expression of *SIMAP3K α* , the member of the MAPK cascade increased after the treatment with 10^{-3} - 10^{-2} M SA and 100-250 mM NaCl in the leaves, but decreased in the root treated with lethal concentration of SA and NaCl. This kinase may participate in the signal

transduction leading to PCD but it can mediate the activation of defence mechanism against oxidative stress at low H₂O₂ levels. One of the most important hallmarks of PCD is the increase in the activity of specific cysteine proteases. The expression of *SICYPI*, the papain-like cysteine protease gene and the *SIMCAI*, the metacaspase gene increased after the treatment with the lethal concentrations of SA and NaCl in the leaves. *SIVPEI* expression was enhanced by the treatment with 10⁻² M SA only in the leaves of tomato plants. This suggests that the lack of the antiapoptotic *SLBII* expression is a characteristic feature of the roots where PCD has been initiated. Since the increased expression of various protease genes can be detected in the leaves, but not in the roots after 24 hours, it can be supposed that changes in protease gene expression occurred earlier in the roots, or the activity of cysteine proteases is controlled at protein level.

7. The protein content in the leaves and roots decreased significantly after the 24h-long treatment with the lethal concentration of SA and NaCl. In parallel, the proteolysis, especially the cysteine protease activity increased in the roots of tomato plants. However, the gelatin-SDS-PAGE did not show protease activity in the leaves, but there were at least 3 putative cysteine protease bands in the roots. It can be concluded that there were significant changes in the protein homeostasis after the changes in the gene expression levels of cysteine proteases. In parallel, there were significant changes in the ion homeostasis of the plants after the treatment with SA and NaCl. The treatment with lethal concentration of SA and NaCl decreased the potassium content in the leaves and roots, but the treatment with 10⁻⁴ M SA increased the potassium level in the leaf and root tissues, which can enhance the stress acclimation of the plants.
8. Signal transduction pathways induced by salt stress and SA have been compared at cell level in tomato cell suspension culture. In tomato suspension cultures a treatment with 250 mM NaCl increased the production of ROS, NO and ET. 10⁻³ M SA-induced cell death was also accompanied by ROS and NO production, but ET emanation, the most characteristic difference between the two cell death programs, did not change. ET synthesis was enhanced by addition of ET precursor 1-aminocyclopropane-1-carboxylic acid (ACC), which after two hours increased the ROS production in the case of both stressors and accelerated cell death under salt stress. However, it did not change the viability and NO levels in SA-treated samples. The effect of ET induced by high NaCl concentration could be blocked with silver thiosulphate (STS), an inhibitor of ET action. STS reduced the death of cells which is in accordance with the decrease in ROS production of cells exposed to high salinity. Unexpectedly, application of STS together with SA resulted in increasing

ROS and reduced NO accumulation which led to a faster cell death. NaCl- and SA-induced cell death was blocked by Ca²⁺ chelator EGTA and calmodulin inhibitor W-7, or with the inhibitors of ROS. The inhibitor of MAPKs, PD98059, and the cysteine protease inhibitor E-64 reduced cell death in both cases. These results show that NaCl induces cell death mainly by ET-induced ROS production, but ROS generated by SA was not controlled by ET in tomato cell suspension. Our results suggest that the decrease of the intracellular K⁺ concentration and K⁺/ Na⁺ ratio is a common phenomenon in triggering programmed cell death by lethal concentrations of SA and NaCl.

9. The ET production in the roots is different from ET production in the suspension culture. ET production decreased in the roots of tomato after the treatment with 10⁻³ és 10⁻² M SA or 250 mM NaCl. In contrast to the results measured in the root, ET increased in the 250 mM NaCl treated cells in the suspension culture. Our results suggest that the cell suspension culture is not a good model of the root meristem cells.

PUBLICATION LIST

Full papers

(Thesis is based on articles marked by *)

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- Ágnes Szepesi, **Péter Poór**, Judit Kovács, Zoltán Takács, Ágnes Gallé, Irma Tari (2013) Effects of salicylic acid on polyamine metabolism in tomato plants. Plant Diseases and Resistance Mechanisms. 2013. február 20-22. Vienna, Austria (poster)
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