Final Report
2011. október 30.
OTKA K 76854

Salicylic acid-induced improvement of of salt stress resistance of tomato: acclimation or programmed cell death

Salicylic acid (SA) has been involved in the acclimation to various abiotic stressors such as chilling, drought or heavy metal stress and could enhance the resistance of plants when it was applied as a chemical hardening in a pre-treatment period before the abiotic stress. However, the improvement of salt tolerance of plants by exogenous SA is somewhat contradictory. Borsani et al. (2001) found that during 100 mM NaCl treatment a greater degree of oxidative damage occurred in the wild type than in the SA-deficient transgenic *Arabidopsis* line expressing a salicylate hydroxylase (*NahG*) gene. This result suggests that, depending on the plant species, mode of application, developmental stage and concentration range, SA may enhance the stress injury of germinating seedlings during salt stress.

Salinity imposes both ionic and osmotic effects on plants. Na^+ influx into the root cells elevates the cytoplasmic Na^+ concentration and causes toxicity symptoms. Salt tolerant species can prevent Na^+ accumulation in the cytoplasm by reducing Na^+ entry into the cell, or by the exclusion of Na^+ from the cytoplasm to the apoplast or into the vacuole. The maintenance of growth and development in saline environment is associated with an osmotic adjustment, and with the synthesis of compatible osmolytes, or in some halophytes with the sequestration and accumulation of Na^+ in the vacuoles. The generation of reactive oxygen species (ROS) also plays a role in the impaired growth under salt stress. Abscisic acid (ABA) proved to be one of the most important hormonal factor in salt stress signalling and a number of salt-responsive genes are strongly induced by ABA. Regulator genes (RD26 and DREB2A), genes coding for the components of signal transduction or genes involved in cellular protection (LEAs with a water-binding, ion-sequestering or chaperone function) were identified among the ABA-dependent or ABA-enhanced early response genes (Fujita et al., 2006). Polyamine (PA) accumulation has also been shown to be an adaptive response of plants under salt stress.

In our earlier OTKA project (OTKA K 038392) it was found that exogenous application of SA resulted in severe water stress in cultivated tomato (*Solanum lycopersicum* cv. Rio fuego), decreased the water potential and the uptake of K^+($^{86}Rb^+$) and resulted in fast stomatal closure in short term experiments. Moreover, treatment of tomato with 10^{-3} M or higher concentrations of SA led to the death of plants. However, when plants were exposed to 10^{-7}-10^{-4} M SA for a three-week-long pre-incubation period they could adapt osmotically, and the plants accumulated both inorganic and organic osmolytes. SA pre-treatment could be considered as a chemical hardening because the pre-treated plants displayed a more effective and faster acclimation to subsequent salt stress than the untreated controls. In accordance with the results of other authors both 10^{-7} and 10^{-4} M SA pre-treatment induced an osmotic adaptation and activated antioxidant enzymes. However, it was found that the harmful effects of high salinity were alleviated only in plants pre-treated with 10^{-4} M SA in long-term experiments. The aim of the present project was to reveal the differences between the effectiveness of lower and higher SA concentrations in the mitigation of salt stress injury and we were also interested in what is the role of ethylene, the ethylene-induced oxidative stress as well as protease activity in the cell death trigger at high SA and NaCl concentrations?

The main scientific results of the project are summarized as follows:

1. The physiological effects of SA on tomato plants under pre-incubation period

1.1. The effect of SA on the photosynthetic activity of plants

SA induces fast stomatal closure in several species and may therefore be expected to affect the rate of photosynthesis. The beneficial effect of SA on photosynthesis may be manifested in a wide array of metabolic and physiological processes. The chlorophyll and carotenoid contents were enhanced by low SA concentrations in various plant species (Hayat *et al*. 2005) and SA treatment also proved to be effective in increasing the pigment content of tomato leaves under salt stress in our experimental system, too (Szepesi et al. 2009). However, the results of Hayat *et al*. (2008) revealed significant declines in the photosynthetic parameters, the leaf water potential, in chlorophyll and relative water contents in response to exogenously applied SA in tomato plants exposed to water stress.

Our results revealed that, in plants grown in 10^{-7} and 10^{-4} M SA-containing culture solution the maximum CO_2 fixation rate (A_{max}) of the CO_2 (A/C_i) and light response (A/PPFD) curves increased slightly in short-term (1 day) experiments. As a result of mild water stress the stomatal conductance decreased under greenhouse conditions at 300 μmol m^{-2} s^{-1} light intensity. However, the effect was only transient and the stomatal conductance and the rate of CO_2 fixation were not significantly different from those of control plants after three weeks of the pre-incubation period (long-term experiments) (Poór et al. 2011).

We detected decreased hexokinase (HXK) activity by using glucose or fructose as substrates in the leaf tissues of tomato plants. Depending on the applied concentration, both short- and long-term application of SA could enhance the total soluble sugar content of the leaf and/or root tissues. This coincided with tissue-specific decreases in HXK activity both in short-term and long-term experiments. Since such treatments may affect the carbohydrate metabolism at several points, we cannot expect a very close correlation with the accumulation of one or more hexose species and hexokinase activity. However, the accumulation of soluble sugars and of sucrose in the roots of plants growing in the presence of 10^{-4} M SA contributed to an osmotic adjustment and to an improved tolerance of the hardened plants to the subsequent salt stress.

SA applied at 10^{-3} M or higher concentration in hydroponic culture decreased the stomatal conductance (g_s), the maximal CO_2 fixation rate (A_{max}) and the initial slopes of the CO_2 (A/C_i) and light response (A/PPFD) curves, the carboxylation efficiency of Rubisco (CE) and the photosynthetic quantum efficiency (Q), respectively and resulted in the death of tomato plants.

1.2.The effect of SA on stomatal movement

It is of great importance that the permanent inhibition of photosynthesis by SA in intact tomato leaves could be detected only at those concentrations (higher than 10^{-4} M) which induced PCD in short period of time. SA at sublethal concentration (10^{-4} M) caused only a transient decline in stomatal conductance and photosynthetic performance (Poór et al., 2011). In contrast to the intact leaves stomata in epidermal peels exhibited a double phase response as a function of increasing SA concentrations, and they closed in the presence of low (10^{-7} M) or extremely high (10^{-3}M) concentration of SA while an intermediate SA level (10^{-4} M) resulted in stomatal opening after 1-hour incubation.

The effect of SA was studied on single guard cell function, on the mechanism of stomatal closure and on the photosynthetic activity of single guard cells in epidermal peels. In our experiments SA was shown first time to induce stomatal opening (Poór et al. submitted). When SA induced the opening of stomatal apertures, H_2O_2 and NO levels, the second messengers of SA-induced signalling in guard cells were at minimum suggesting that these

molecular species may effectively scavenge each other (one of the major reactions of nitric oxide is the reaction with superoxide to form peroxynitrite) or their synthesis is inhibited in some way or another. This new balance of reactive molecular species may cause the opening of stomata at 10^{-4} M SA concentration. Based on the effects of specific inhibitors, SA-induced stomatal closure at 10^{-7} and 10^{-3} M was mediated by reactive oxygen species (ROS) and NO. However, the mechanisms leading to closing of stomata seem to be different in case of low and high SA concentrations. The effectiveness of salicylhydroxamic acid (SHAM) to prevent the stomatal closure induced by 10^{-7} M SA suggests the involvement of extracellular peroxidases in ROS production. At 10^{-3} M SA concentrations the accumulation of ROS occurred preferentially in guard cell chloroplasts. It can be assumed that the presence of these reactive molecular species shows a significant decline in guard cell photosynthesis at 10^{-3} M SA. Thus, closure of stomatal apertures at high SA concentration is mainly dependent on intracellular ROS. It can be supposed that the ATP synthesis declines in guard cell chloroplasts with severely damaged reaction centres and with reduced linear electron transport rate. This constrains the recovery process, the activation of ATP-ases at the plasma membrane, which is the prerequisite of active ion uptake during stomatal opening. The permanent closure of stomata may contribute to the photooxidative damage in leaf tissues and can make it more serious and irreversible. We would like to emphasise that the effect of SA on guard cell photosynthesis can determine the successful acclimation of plants to various stressors or it may contribute to initiation of programmed cell death (PCD) of leaf tissues.

1.3.The effect of SA on aldose reductase activity and sorbitol accumulation

Increased aldose reductase (ALR) activities were detected in the leaf tissues of tomato plants grown for 3 weeks in culture medium containing 10^{-7} or 10^{-4} M salicylic acid (SA), and in the roots after the 10^{-4} M SA pre-treatment. The ALR activity changed in parallel with the sorbitol content in the leaves of the SA-treated plants. DEAE cellulose anion-exchange column purification of the protein precipitated with 80 % $(NH_4)_2SO_4$ revealed two enzyme fractions with ALR activity in both the leaf and the root tissues. The fraction of the leaf extract that was not bound to the column reacted with glucose and glucose-6-P as substrates, whereas glucose was not a substrate for the bound fraction or for root isoenzymes. The root enzyme was less sensitive to salt treatment: 50 mM NaCl caused 30 % inhibition in the leaf extract, whereas the enzyme activity of the root extract was not affected. It is suggested that increased ALR activity and sorbitol synthesis in the leaves of SA-treated tomato plants may result in an improved salt stress tolerance.

1.4. *Accumulation of reactive oxygen species (H_2O_2, $^{\bullet}O_2^-$), and nitric oxide (NO) as well as the activation of enzymatic and non enzymatic antioxidant systems during the SA-induced hardening process*

SA has been shown to induce ROS production by increasing the plasmamembrane (PM)-localized NADPH oxidase activity or inhibiting the activity of catalase (CAT), an enzyme that degrades H_2O_2 to H_2O and O_2. SA treatment however does not always lead to H_2O_2 accumulation. Changes in H_2O_2 content were analysed as a function of time in the leaf and root tissues of intact tomato after SA application. It was found that the accumulation of H_2O_2 was significantly enhanced after 24 h on 10^{-4}-10^{-2} M SA treatment in the leaf tissues and on 10^{-3} M SA treatment in the roots. After 3 weeks, before the exposure to high salinity, no significant differences in H_2O_2 content could be detected in the leaves treated with 10^{-7}-10^{-4} M SA as compared with the controls. It has also emerged, that 10^{-2} and 10^{-3} M SA treatments resulted in the death of plants later, with very significant reductions in the viability of the

tissues in the 24-h samples. The NO level in the apical segments of roots increased also as a function of SA concentration and proved to be transient (Gémes et al. 2011).

Most of ROS generated by SA is produced in the apoplast by a PM-associated NADPH oxidase. We found that 10^{-7}-10^{-4} M SA concentrations as well as 200 mM NaCl increased the expression level of NADPH oxidase determined by semiquantitative RT-PCR. We also found higher enzyme activity quantified by extracellular production of superoxide in the leaves treated with SA or in tomato protoplasts under salt stress.

In the the meristematic zones of root tissues the ROS level increased in parallel with the NO content, in plants exposed to lethal, 10^{-3} or 10^{-2} M SA which led to a fast decrease in the cell viability of the apical tissues.

The changes of antioxidant enzyme activities showed only a transient increase under the pre-incubation period which is in accordance with the definition of priming. This pre-adaptation does not mean a constitutive expression and activity of genes and enzymes participating in the defence reactions but it means a faster activation of the defence system when plants are exposed to the second stressor. We found a transient increase in the extractable activity of the enzymes participating in ROS scavenging such as catalyse (CAT) or superoxide dismutase (SOD). Similar tendencies could be observed in the activity of the enzymes participating in the Halliwell-Asada-Foyer ascorbate-glutathione cycle. With the exception of glutathione reductase (GR) in the leaves, all of the enzyme activities declined to the control values or below in the leaf and root tissues of plants pre-treated with 10^{-4} M SA (Tari et al. 2011). However, at the end of the pre-treatment period, plants contained higher amount of non-enzymatic antioxidants, glutathione and especially ascorbate than the unhardened controls.

1.5.Effect of SA pre-treatment on the concentration of various plant hormones an plant growth regulators

It was revealed that abscisic acid (ABA) began to accumulate when the tomato plants were exposed to SA. Unexpectedly, ABA content remained significantly higher in the leaves and in the roots of plants exposed to 10^{-4} M SA until the end of three-week-long pre-incubation period. The application of 10^{-4} M, but not of 10^{-7} M SA, led to prolonged ABA accumulation and to an enhanced activity of aldehyde oxidase (AO1, EC.1.2.3.1.). This enzyme is responsible for the conversion of ABA-aldehyde to ABA, both in root and leaf tissues. AO2-AO4 isoforms from the root extracts also exhibited increased activities (Szepesi et al. 2009).

The enhanced polyamine (PA) and ABA concentrations may moderate the ionic effects of Na^+ on the plasma membrane during salt stress. In plants pre-treated with 10^{-4} M SA there were increases in putrescine level in the leaves and in putrescine and spermidine content in the root tissues (Szepesi et al. 2009). Similar changes in the PA pattern were also observed in *Lycopersicon pennellii*, a wild halophyte relative of tomato under salt stress (Santa-Cruz et al. 1999). Thus SA pre-treatment shifted the PA content of tissues toward a halophyte character.

Although the ethylene production of tissues has continually changed from time to time, SA has not reduced the ethylene release from the leaf and root tissues in 10^{-7}-10^{-4} M SA concentration range. Moreover, higher concentrations significantly induced the synthesis of ethylene in parallel with PCD trigger.

The role of SA-induced ethylene production and signalling in the acclimation to salt stress and in the PCD trigger was investigated in tomato *Never ripe* mutants which has a mutation in the ethylene receptor, and as a consequence in ethylene signalling.

The pattern of SA-induced production of ROS and NO were different in the apex of adventitious roots in wild-type and in the ethylene-insensitive *Never ripe* (*Nr*) mutants of

tomato (*Solanum lycopersicum* L. cv. Ailsa Craig). ROS were up-regulated, while NO remained at the control level in apical root tissues of wild-type plants exposed to sublethal concentrations of SA. In contrast, *Nr* plants expressing a defective ethylene receptor displayed a reduced level of ROS and a higher NO content in the apical root cells. In wild-type plants NO production seems to be ROS(H_2O_2)-dependent at cell death-inducing concentrations of SA, indicating that ROS and NO may interact to trigger oxidative cell death. In the absence of significant ROS accumulation, the increased NO production caused moderate reduction in cell viability in root apex of *Nr* plants exposed to 10^{-3} M SA. This suggests that a functional ethylene signalling pathway is necessary for the control of ROS and NO production induced by SA (Tari et al. 2011).

1.6. Investigation of the programmed cell death induced by SA and NaCl in leaf protoplast and tomato cell suspension cultures

In order to evaluate the effect of SA on the accumulation of intracellular ROS and NO, protoplasts were prepared and incubated with SA in 10^{-7}-10^{-3} M concentration range. The data indicated rapid, significant and transient increases in ROS production after treatment with 10^{-7} and 10^{-4} M SA. Although the intracellular ROS production of the protoplasts increased significantly after 2.5 h of incubation in SA-containing solution, the oxidative burst could be detected only at 10^{-3} M, the PCD-inducing concentration of SA. This increase was partially sensitive to diphenylene iodonium (DPI), an inhibitor of NADPH oxidase. However, DPI, a chemical that covalently attaches to the reaction centres of flavin-containing enzymes such as NADPH oxidases proved to be not very specific. It is also used as an inhibitor of animal NOS, although the plant homologues of this enzyme have not yet been found. In our experiments,- with the exception of highest SA concentrations-, NO production was not inhibited by DPI. This is in accordance with the finding of other authors that NO generation is generally detected under conditions in which H_2O_2 production is also enhanced (Gémes et al. 2011).

All of the growth-regulating compounds (putrescine, spermidine, spermine, ABA and the immediate precursor of ethylene, 1-aminocyclopropane-1-carboxylic acid (ACC) resulted in an increase in the intracellular ROS production of the protoplasts, which were significantly inhibited by DPI. After 2.5 h high levels of NO were detected under all of the treatments, which increased further in the presence of ACC. The elevated NO levels were reduced when 10 μM DPI was applied in the incubation buffer suggesting that the induction of NO accumulation was controlled by ROS. Addition of spermidine, spermine, ABA and ACC decreased, whereas treatment with putrescine did not reduce the viability of tomato protoplasts (Gémes et al. 2011).

In contrast to our expectations, tomato cell suspension culture cannot be considered as a model system of heterotrophyc plant tissues such as roots. The data obtained with cell suspension does not match the results obtained with intact roots. However, we measured interesting data concerning the PCD induction by an abiotic (high salinity) and a biotic stressor (SA) at cell level.

Salt stress- and salicylic acid (SA)-induced cell death can be triggered by different signalling pathways (Poór et al. 2012 (accepted)). 250 mM NaCl and 10^{-3} M SA caused the death of tomato suspension cells within 6 hours which was accompanied by DNA fragmentation. Treatment with 250 mM NaCl increased the production of ROS, NO and ethylene. SA-induced cell death was also accompanied by ROS and NO production, but ethylene emanation from cells, the most characteristic difference between the two cell death programs, did not change. Ethylene synthesis was enhanced by addition of ethylene precursor ACC, which after two hours increased the ROS production in case of both treatments but did not change NO levels in SA-treated samples. The enhanced levels of ROS production

especially in salt stressed cells led to an increase in cell death. The effect of ethylene induced by salt stress could be blocked with silver thiosulphate (STS), an inhibitor of ethylene action. STS reduced the death of cells which is in accordance with the decrease in ROS production of cells exposed to high salinity. However, application of STS together with SA resulted in increasing ROS and reduced NO accumulation which led a faster cell death. ACC in SA-treated cells did not increase NO accumulation and this was reduced further by STS. The role of various signalling pathways in NaCl- and SA-induced cell death was revealed by the application of appropriate inhibitors. Our results show that supraoptimal concentration of NaCl induces cell death by generating oxidative stress and inducing ethylene production, on the other hand SA induces cell death mainly by generating oxidative stress (Poór et al. submitted). The expression pattern and the activity of various types of proteases changed characteristically in cells exposed to high salinity or to lethal concentration of SA.

2. The effect of SA pre-treatments on tomato under salt stress

2.1.Effect of SA on the photosynthetic activity of plants and on the accumulation of compatible osmolytes under salt stress

The beneficial effect of SA on the photosynthetic performance in tomato could be detected only under salt stress. These plants exhibited higher maximal CO_2 fixation rate (A_{max}) and the initial slopes of the CO_2 (A/C_i) and light response (A/PPFD) curves, the carboxylation efficiency of Rubisco (CE) and the photosynthetic quantum efficiency (Q) were also higher in pre-treated plants exposed to high salinity. This means that the plants could maintain higher maximal photosynthetic capacity at saturating C_i and light intensity values, and the significantly enhanced CE values indicated that the carboxylase activity of Rubisco is more efficient under CO_2-limited conditions in plants exposed to high salinity (Poór et al. 2011).

The HXK activity decreased further under high salinity in both leaves and roots. Apart from its putative role in delaying senescence, a decreased HXK activity may divert hexoses from catabolic reactions to osmotic adaptation and in these tissues the decreases in activities of glucokinase and fructokinase may promote the accumulation of soluble sugars in the leaves under salt stress. Salt stress elicited by 100 mM NaCl enhanced the accumulation of sorbitol in the leaves of control plants and as compared with the untreated control the sorbitol content in the SA pre-treated leaves remained elevated under salt stress (Tari et al. 2010). However, on whole cell basis, the concentration of sorbitol was present in osmotically irrelevant amount in tissues of stressed tomato. Sorbitol, a compatible solute, may play an important role in the osmotic balance of cell compartments. The highest concentrations of sorbitol has been found in the chloroplast stroma of common plantain, sea plantain and peach plants (Nadwodnik and Lohaus 2008), suggesting that sorbitol may contribute to cell structure protection and osmotic adaptation of this compartment.

2.2.Effect of SA on the accumulation of Na^+ and other inorganic osmolytes under salt stress

Under salt stress elicited by 100 mM NaCl the pre-treatments decreased the Na^+ content in the roots and enhanced that in the shoot tissues, suggesting that SA facilitated the long-distance transport of Na^+ into the leaves. The accumulation of Na^+ and its contribution to the osmotic potential in the leaf tissues of apparently healthy plants suggested that the salt stress response after 10^{-4} M SA pre-treatment in *S. lycopersicum* plants was similar to that observed in the salt tolerant wild relative of tomato, *Lycopersicon pennellii*. As indicated by the enhanced

concentrations of ROS-scavenging compounds, such as carotenoids in the leaves and polyamines (PAs) in the root tissues of tomato plants pre-treated with 10^{-4} M concentration of SA, the salt stress response of *Solanum lycopersicum* became similar to that of a highly salt tolerant wild genotype, *L. pennellii*. These changes could not be detected in plants exposed to lower SA concentrations (Szepesi et al. 2009).

2.3. *Accumulation of reactive oxygen species (H_2O_2, $^{\bullet}O_2^-$), and nitric oxide (NO) as well as the activation of enzymatic and non enzymatic antioxidant systems during the SA-induced hardening process under salt stress*

High amount of H_2O_2 accumulated in the leaf cells after a 1-week exposure to 100 mM NaCl. This was not increased further, but was significantly reduced in the plants pre-treated with SA. Similar results were found after staining the tissues with diaminobenzidine, which generates a brown reaction product with H_2O_2. 100 mM NaCl also enhanced ROS and NO levels in the apical region of roots, but the production of these reactive molecular species was inhibited or they were effectively scavenged in the root apices pre-treated with SA. The viability of the cells demonstrated by fluorescein diacetate staining, did not decrease under high salinity in the presence of SA.

Although the plants pre-adapted with 10^{-7} M SA were able to increase the activity of a number of antioxidant enzymes, such as peroxidase (POD), SOD and glutathione reductase activity in the young leaves, they cannot successfully acclimate to moderate salt stress induced by 100 mM NaCl and the plants displayed senescence symptoms. The plants pre-treated with 10^{-4} M SA, however, could enhance the activity of ascorbate peroxidase (APX) and GR in the root tissues and were able to maintain a significantly enhanced level of non-enzymatic antioxidants, ascorbate and glutathione in the roots which remained high under salt stress.

2.4.Changes in gene expression: genes participating in the biosynthesis of ABA and accumulation of glutathione transferase/peroxidase isoenzymes

ABA plays essential role in the stress adaptation by modifying a number of gene expressions including those which participates in its own biosynthesis. Zeaxanthin epoxidase (ZEP), epoxicarotenoid dioxygenase (NCED) and aldehyde oxidases (AOs) may contribute to stress-induced ABA accumulation, because they catalyze the control points of ABA biosynthesis. The expression levels of the known tomato ZEP, NCED and AO genes were monitored by quantitative real-time PCR (QRT-PCR) after 3-week pre-treatment with two salicylic acid (SA) concentrations followed by 1-week-long salt stress. The 10^{-4} M SA pre-treatment, but not the 10^{-7} M SA, increased the *Sl*ZEP and *SlAO2* gene expression in the roots, and both SA concentrations increased the transcript amount of *Sl*NCED *and SlAO3*. This was in accordance with the significantly elevated ABA content of the root tissues, which was unexpected in a long-term experiment. However, one-week-long treatment with 100 mM NaCl decreased the expression of ABA biosynthetic genes. These changes in the gene expressions and enzyme activities which maintain high ABA content both in leaves an root tissues may contribute to the successful acclimation of 10^{-4} M SA pre-treated tomato plants to subsequent salt stress (Horváth et al. 2011).

The activities of glutathione transferase (GST), glutathione peroxidase (GPOX) and dehydroascorbate reductase (DHAR) were also analyzed spectrophotometrically after one week of salt stress. All of these activities represent a GST enzyme family, but the changes did not show convincing tendencies at the end of the pre-treatment period (Csiszár et al. 2001a). SA enhanced the GPOX activity to a highest extent. The salt treatment enhanced the activity

of GSTs in the fully expanded leaves and roots and in the SA pre-treated plants the GST and GPOX activities has been increased further under salt stress. We found significant increases in the transcript abundance of *Sl*GSTU5, *Sl*GSTU25 and *Sl*GSTF8 isoenzyme in the roots of SA pre-treated plants. The expression of these genes remained elevated under salt stress in plants hardened by SA which may indicate a much better detoxifying capacity of these plants under high salinity (Csiszár et al. 2001b).

General evaluation of the project

All of the scientific tasks have been finished and the experimental work planned in the project has been completed.

The work of two MSc students was planned in the proposal. They were not included in the project by name. Fortunately, they have got a PhD scholarship in the Doctoral School of Biology at University of Szeged. One of them, Péter Poór was included in the staff of the project officially, and Katalin Gémes also made her PhD thesis on this topic. She has not been officially a staff member. Finally, two MSc diploma works (Edit Horváth, 2009; and Dóra Szopkó, 2011) as well as two PhD theses were completed from the scientific results of the project. One of the PhD Theses has already been defended (Katalin Gémes, 2011).

In the Investments row: two laptops were purchased.

The leader of the project (Irma Tari (TI) and Péter Poór (PP) participated in the XVIII Congress of European Societies of Plant Biology, 4-9 July, Valencia Spain. PP won a student travel grant for FESPB which reduced his budget. TI participated in the 10th International Conference on Reactive Oxygen and Nitrogen Species in Plants, July 5-8, 2011, Budapest, Hungary. TI, Csiszár Jolán (CSJ) and PP participated in the conferences Plant Abiotic Stress Tolerance, Vienna, Austria, 8-11 February 2009, and Molecular Aspects of Plant Development, February 23-26 2010, Vienna, Austria, as well as in the 10th Congress of the Hungarian society for Plant Biology, August 31- Sept 2, Szeged.

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Konferenciák

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