



Exogenous spermidine affects polyamine metabolism in salinity-stressed *Cucumis sativus* roots and enhances short-term salinity tolerance

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Summary

We investigated the effects of short-term salinity stress and spermidine application to salinized nutrient solution on polyamine metabolism and various stress defense reactions in the roots of two cucumber (*Cucumis sativus* L.) cultivars, Changchun mici and Jinchun No. 2. Seedlings grown in nutrient solution salinized with 50 mM NaCl for 8 d displayed reduced relative water content, net photosynthetic rates and plant growth, together with increased lipid peroxidation and electrolyte leakage in the roots. These changes were more marked in cv. Jinchun No. 2 than in cv. Changchun mici, confirming that the latter cultivar is more salinity-tolerant than the former. Salinity stress caused an increase in superoxide and hydrogen peroxide production, particularly in cv. Jinchun No. 2 roots, while the salinity-induced increase in antioxidant enzyme activities and proline contents in the roots was much larger in cv. Changchun mici than in cv. Jinchun No. 2. In comparison to cv. Jinchun No. 2, cv. Changchun mici showed a marked increase in arginine decarboxylase, ornithine decarboxylase, S-adenosylmethionine decarboxylase and diamine oxidase activities, as well as free spermidine and spermine, soluble conjugated and insoluble bound putrescine, spermidine and spermine contents in the roots during exposure to salinity. On the other hand, spermidine application to salinized nutrient solution resulted in alleviation of the salinity-induced membrane damage in the roots and plant growth and photosynthesis inhibition, together with an increase in polyamine and proline contents and antioxidant enzyme activities in the roots of cv. Jinchun

Abbreviations: ADC, agrinine decarboxylase; CAT, catalase; DAO, diamine oxidase; F_v/F_m , the maximum photochemical efficiency of PSII; ODC, ornithine decarboxylase; PAO, polyamine oxidase; P_n , net photosynthetic rates; POD, peroxidase; PSII, photosystem II; Put, putrescine; RWC, relative water content; SAMDC, S-adenosylmethionine decarboxylase; SOD, superoxide dismutase; Spd, spermidine; Spm, spermine.

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No. 2 but not of cv. Changchun mici. These results suggest that spermidine confers short-term salinity tolerance on cucumber probably through inducing antioxidant enzymes and osmolytes.

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Introduction

Polyamines are ubiquitous low-molecular-weight aliphatic amines that are involved in regulation of plant growth and development (Martin-Tanguy, 2001). Because of their polycationic nature at physiological pH, polyamines are able to interact with proteins, nucleic acids, membrane phospholipids and cell wall constituents, thereby activating or stabilizing these molecules. The most commonly found polyamines in higher plants, the diamine putrescine (Put), the triamine spermidine (Spd) and the tetraamine spermine (Spm) may be present in the free, soluble conjugated and insoluble bound forms. Soluble conjugated polyamines are those which are covalently conjugated to small molecules such as phenolic compounds, and insoluble bound polyamines are those which are covalently bound to macromolecules such as nucleic acids and proteins. Transglutaminase (EC 2.3.2.13) is a key enzyme, which transforms free polyamines into insoluble bound polyamines. This enzyme covalently links polyamines to endoglutamines of proteins to play an important role in the post-translational modifications of proteins. In plants, the key enzymes in polyamine are arginine decarboxylase (ADC, EC 4.1.1.19), ornithine decarboxylase (ODC, EC 4.1.1.17) and S-adenosylmethionine decarboxylase (SAMDC, EC 4.1.1.50). Put can be synthesized directly by decarboxylation of ornithine (catalyzed by ODC), or indirectly by decarboxylation of arginine (catalyzed by ADC) via agmatine and N-carbamoylputrescine intermediates. Spd and Spm are synthesized from Put by successive addition of aminopropyl groups from decarboxylated S-adenosylmethionine that is derived from S-adenosylmethionine (SAM) by the action of SAMDC. Polyamine degradation is catalyzed by diamine oxidase (DAO, EC 1.4.3.6) and polyamine oxidase (PAO, EC 1.5.3.3). Recent studies have focused on the involvement of polyamines in the defense reaction of higher plants to various environmental stresses (Bouchereau et al., 1999).

Salinity is one of the major environmental factors limiting plant growth and yield (Parida and Das, 2005). Salinity imposes two constraints on plants: the hyperosmotic effect (especially short-term stress) due to lower soil water potential, and the hyperionic effect (especially long-term stress) due

to direct toxicity of ions over metabolism and nutrition of plants. When plants are subjected to salinity, reactive oxygen species such as superoxide, hydrogen peroxide, singlet oxygen and hydroxyl radicals accumulate rapidly (Verma and Mishra, 2005). These free radicals disrupt normal metabolism through peroxidizing membrane lipids and denaturing proteins and nucleic acids. Plants have evolved various defense mechanisms to cope with the potential damage of salinity. These include accumulation of osmolytes such as proline, glycinebetaine and sugars, and up-regulation of antioxidant enzymes as well as Na⁺/H⁺ antiporters (Parida and Das, 2005). A salinity-induced increase in the endogenous polyamines has also been reported in various plants (Das et al., 1995; Chattopadhyay et al., 2002). It is well established that enhanced polyamine biosynthesis can protect plants from salinity by scavenging free radicals, stabilizing membrane and cellular structures, maintaining a cation–anion balance (Bouchereau et al., 1999), modulating ion channels (Lopatin et al., 1994) and energizing the cell through stimulation of ATP synthesis (Ioannidis et al., 2006).

Numerous attempts have been made to improve the salinity tolerance of a variety of crops by traditional breeding programs, but commercial success has been limited thus far. In recent years, some methods, such as transgenic approaches and exogenous polyamine application, have been directed towards the agricultural use of polyamine ability for enhancing the salinity tolerance of plants. Several transgenic approaches have shown enhanced salinity tolerance in transgenic rice, sweet potato, tobacco and *Arabidopsis thaliana* plants that overexpress polyamine biosynthetic enzyme genes (Roy and Wu, 2001; Kasukabe et al., 2004, 2006; Wi et al., 2006). However, the complex regulation of polyamine synthesis in relation to endogenous substrate availability, developmental stages and organ-specific parameters has handicapped the achievement of practical transgenic results (Ndayiragije and Lutts, 2006). Alternatively, exogenous polyamine application is a convenient and effective approach for enhancing salinity tolerance of crops and eventually improving crop productivity under high salinity. Indeed, exogenous polyamine application has been successfully used for enhancing salinity tolerance of plants

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