

POLYAMINE ANALYSIS OF *SOLANALES* CROP PLANT ORGANS INCLUDING ROOT-KNOT GALL AND TUBER-POWDERY SCAB

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ABSTRACT

Polyamines acid-extracted from the buds, roots, stems, leaves, flowers, fruits and seeds of five *Solanales* crop plants were analyzed by high-performance liquid chromatography and gas chromatography. Endogenous concentrations of polyamines per wet weight of the organs were calculated. Putrescine, spermidine and spermine were the major common polyamines of the *Solanales* organs. Homospermidine and aminopropylhomospermidine were detected abundantly in tomato and eggplant roots. Diaminopropane, cadaverine, norspermidine, norspermine and thermospermine were detected in a minor polyamine in some organs. Skins of tomato and eggplant fruits showed lower polyamine levels, whereas skins of potato tubers and sweet potato tuberous roots showed higher polyamine levels. The root-knot galls caused by a nematode in the tomato and eggplant roots, and the tuber-powdery scabs caused by a cercozoan in potato tuber were increased in putrescine and spermidine (and putrescine) contents.

Keywords: eggplant, polyamine, potato, root-knot gall, powdery scab, tomato

INTRODUCTION

By the transgenic studies of cellular polyamine synthetic and catabolic enzymes using a model plant, *Arabidopsis thaliana*, it has been proved that spermidine, spermine and thermospermine are involved in plant cell proliferation and differentiation and play a defensive role against various stresses (Kusano et al. 2008, Takahashi and Kakehi 2010, Naka et al. 2010, Minocha et al. 2014). We have analyzed directly endogenous polyamines including unusual polyamines such as homospermidine, norspermidine, aminopropylhomospermidine and norspermine in the seeds and seedlings of the crop plants belonging to the families *Fabaceae* (formerly *Leguminosae*) and *Poaceae* (formerly *Gramineae*) (Hamana et al. 1994, 1996) and the various

organs of *Brassica* crop plants (Hamana et al. 2015). On the other hand, polyamine levels of the leguminous root nodules, caused by the infection of the bacteria *Bradyrhizobium* or *Rhizobium* (Fujihara 2009) and the clubroots of *Brassica* plants, caused by the infection of a cercozoan, *Plasmodiophora brassicae* (Hamana et al. 2015) were determined to know its symbiotic or parasitic effects on the polyamine profiles of host plant roots.

In the order *Solanales*, fruit of *Solanum lycopersicum* (formerly *Lycopersicon esculentum*) (tomato), *Solanum melongena* (eggplant) and *Capsicum annuum* (pepper), and tuber (subterranean stem) of *Solanum tuberosum* (potato), and tuberous root (root tuber, storage root) of *Ipomoea batatas* (sweet potato) are worldwide useful crops. Root-knot galls caused by the infection of the nematode *Meloidogyne incognita* are found frequently in the roots of tomatoes and eggplants. Powdery scab is an economically severe disease of potato tubers caused by the infection of cercozoan, *Spongospora subterranea* (Gau et al. 2013). Polyamine profiles in the root-knot galls and the tuber-powdery scabs were determined in the present study to analyze possible role(s) of polyamines against the microbe infection.

Because ingestion of polyamines in food has been proposed to combat the decrease in mammalian cellular polyamine levels caused by aging, analysis of polyamine profiles of crop plant organs contributes as nutritional information in addition to the presentation of phylogenetic polyamine distribution catalogue in higher land plants (Hamana et al. 2015). Endogenous polyamine levels in the root, tuberous root, tuber, bud, stem, leaf, fruit and seed were analyzed in five *Solanales* crop plants to survey the organ-specific polyamine profile and organ-advantage for polyamine ingestion.

MATERIALS AND METHODS

***Solanales* plant organs**

Young healthy roots and leaves were harvested from the young plants of tomato (mini-tomato) (cultivar “Mini-carol”) and eggplant (long egg form-eggplant) (“Senryo-2”) (30 days after sowing) purchased in May from Noguchi Nursery Co. Maebashi, Gunma, Japan. The young plants were cultivated for four months in the two experimental field brocks of an outdoor farm, Kuroiwa Survey Design Office Co., Maebashi. Infected roots grown in the soil brock growing the root-knot nematode *Meloidogyne incognita* were harvested in September. Normal roots and root-knot galls were separated from the infected roots. Mature tomato and eggplant fruits were harvested in August from the healthy plants in the farm. Fresh fruits of another cultivar of mini-tomato (“Senka”) and eggplant (“Kuromasari”), and fresh fruits of bell pepper (“Kyunami”) and sweet pepper (“Shishitou”) cultivated in outdoor farms in Maebashi were purchased in August. Abnormal crowding white hairy roots of tomato were obtained on July 11, 2015 from the mature

mini-tomato plant (“Mini-carol”) growing in a small pot in JA-Maebashi, Gunma. Seeds of the two cultivars of mini-tomato and eggplant were purchased from a seed store for sowing, Takii Seeds and Plants Co., Kyoto, Japan. Tubers of potato (“Kitaakari”, “Beniakari” and “Shirowase”) and tuberous roots of sweet potato (“Beniazuma”) were harvested in September (four months after planting a piece of tuber or tuberous root in May) from Hamana’s gardens in Tsumagoi, Gunma and Takasaki, Gunma, respectively. Their leaves, stems and fruits were harvested in August. Buds appeared on the tubers and tuberous roots harvested in the previous year were obtained in May. Infected potato tubers (‘Kitaakari’) with powdery scab lesions were supplied on October 2, 2014 from Hokkaido Agricultural Research Center, National Agriculture and Food Research Organization (NARO), Sapporo, Japan.

Polyamine analysis

The plant organs (10-100g) were homogenized in the same weight of 10% (1.0 M) perchloric acid (PCA) by a mixer. After extraction with 5% PCA three times, the polyamines in the PCA extracts were concentrated by the column of a cation-exchange resin, DOWEX W50x8 (Hamana et al. 2015, 2016a, 2016b). The concentrated polyamines including agmatine, histamine and methylated polyamines were analyzed by high-performance liquid chromatography (HPLC) on a Hitachi L6000 (Hamana et al. 2015, 2016a, 2016b). High-performance gas chromatography (HPGC) on a SHIMADZU GC-17A and HPGC-mass spectrometry (HPGC-MS) on a JEOL JMS-700 were performed after heptafluorobutyrylation of the concentrated polyamines (Niitsu et al. 2014, Hamana et al. 2015, 2016a, 2016b). Molar concentrations of endogenous polyamines per gram of wet weight of organ ($\mu\text{mol/g w.w.}$) estimated from the HPLC and HPGC analyses are shown in Table 1 as a list of names, structures and abbreviations of the *Solanales* organ polyamines.

RESULTS AND DISCUSSION

1. Polyamines in various organs of tomato, eggplant, pepper, potato and sweet potato

Among *Solanales* organs, the fruits of bell peppers and sweet peppers are rich in spermine (0.70-0.93 $\mu\text{mol/g w.w.}$), agmatine (0.15 $\mu\text{mol/g w.w.}$) and cadaverine (0.13 $\mu\text{mol/g w.w.}$). For nutritional polyamine intake, the fruit of peppers have an advantage on the spermine content rather than tomato fruit (0.18 $\mu\text{mol/g w.w.}$) and eggplant fruit (0.50 $\mu\text{mol/g w.w.}$).

The skin of tomato and eggplant fruits has a lower level of homospermidine and spermine in comparison with their peeled fruits, suggesting that the levels of the two polyamines in the surface skin were possibly down due to atmospheric and photochemical oxidation stresses.

A high amount (0.08 $\mu\text{mol/g}$ w.w.) of thermospermine, which is required for stem elongation in higher plants (Kakehi et al. 2008), was found in the stems of young eggplants, whereas its roots and leaves had a concentration of 0.01-0.03 $\mu\text{mol/g}$ w.w..

Endogenous histamine was extracted into the 5 % PCA and detected selectively in the buds of the potato (0.25 $\mu\text{mol/g}$ w.w.), and identified by our HPLC and HPGC, whereas it was not detectable (< 0.005 $\mu\text{mol/g}$ w.w.) in the buds of the sweet potato as well as that of other organs of the five *Solanales* plants.

2. Polyamines of root and root-knot gall in tomato and eggplant

Among the organs of the mature healthy tomatoes and eggplants, the roots were rich in homospermidine (0.30 and 0.15 $\mu\text{mol/g}$ w.w., respectively) and contained aminopropylhomospermidine (0.06 and 0.01 $\mu\text{mol/g}$ w.w., respectively). Homospermidine widespread in land plants (Hamana et al. 1994, 1996, Shaw et al. 2010) is known as a polyamine of the first pathway of plant alkaloid biosynthesis, and is produced from two putrescines or putrescine plus spermidine by homospermidine synthase (Ober and Hartmann 1999). The abundant occurrence of homospermidine in *Solanales* roots as well as *Brassicales* roots (Hamana et al. 2015) is assumed to be synthesized aminopropylhomospermidine from homospermidine in the roots. The crowding hairy roots of the mature tomato plant grown in a small pot contained diaminopropane, norspermidine and norspermine whereas lower levels of homospermidine and aminopropylhomospermidine levels were suppressed in the hairy roots. It is possible that diaminopropane and norspermidine were produced by polyamine oxidase(s) from spermidine, spermine and thermospermine, and then norspermine was produced from norspermidine in the crowing hairy roots.

In the nematode-infected tomato, putrescine and spermidine levels increased (0.35 to 0.54 $\mu\text{mol/g}$ w.w. and 1.37 to 1.74 $\mu\text{mol/g}$ w.w., respectively) whereas homospermidine, spermine and aminopropylhomospermidine levels decreased (0.62 to 0.31 $\mu\text{mol/g}$ w.w., 0.71 to 0.29 $\mu\text{mol/g}$ w.w. and 0.18 to 0.03 $\mu\text{mol/g}$ w.w., respectively) in the root-knot galls after the infection. In the nematode-infected eggplant, the spermidine level found in the normal root rather increased (1.22 to 1.62 $\mu\text{mol/g}$ w.w.) whereas the spermine levels decreased (0.33 to 0.18 $\mu\text{mol/g}$ w.w.) in the root-knot galls. The relative high level of spermidine content in the normal roots outside the root-knot galls may be a response to the infection of nematode. In comparison to non-infected healthy roots, the normal root region of the infected tomato roots showed a relatively high amount of homospermidine and aminopropylhomospermidine suggesting accumulation of these polyamines in the normal region of the infected tomato roots.

N^1 -methylputrescine (0.03 $\mu\text{mol/g}$ w.w.), N^1, N^4 -dimethylputrescine (0.05 $\mu\text{mol/g}$ w.w.), N^1 -methylhomospermidine (0.03 $\mu\text{mol/g}$ w.w.) and N^1, N^9 -dimethylhomospermidine (0.05 $\mu\text{mol/g}$ w.w.) found in the mature healthy tomato root (Niitsu et al. 2014) were also detected in the root-knot galls of the tomatoes, however, their contents in the root-knot galls showed that half of them were found in the healthy roots, respectively (data not shown), indicating that their level was down after the infection of root-knot nematodes.

Root-knot nematode, root-lesion nematode, cyst forming nematode, stem-gall forming nematode and dagger nematode are known as plant parasites (Blaxter et al. 1998). A plant root-parasitic nematode *Pratylenchus vulnus* (order *Tylenchida*) as well as free-living (bacteriovore) *Caenorhabditis elegans* (order *Rhabditida*) and *Dorylaimus fodori* (order *Dorylaimida*) contained putrescine and spermidine (Hamana et al. 2006). *Meloidogyne incognita* (order *Tylenchida*) cells isolated from the root-knot galls used for polyamine analysis were not abundant enough to detect polyamine, indicating that nematode polyamines were not contaminated into the root-knot gall polyamines in the present study. Although it has been reported that cyst-forming nematodes target spermidine synthase in *Brassicaceae* plants and root-knot nematode effectors modify the polyamine signaling in tomatoes (Hewezi and Baum 2013, Hewezi et al. 2010), the present study is the first to provide details on cellular polyamine changes in tomatoes and eggplants with root-knot nematode infection.

3. Polyamines of tubers and tuber-powdery scabs in potato and tuberous roots in sweet potato

Low levels of spermine (0.12-0.16 $\mu\text{mol/g}$ w.w.) were observed in the healthy potato tubers, whereas high levels of spermine (0.80-1.08 $\mu\text{mol/g}$ w.w.) were observed in the healthy sweet potato tuberous roots, indicating that sweet potato tuberous roots have a nutritional advantage on spermine content.

When the potato and sweet potato were peeled, the skin parts of the tubers and the tuberous roots contained 1.5-2 folds of the putrescine, spermidine and spermine levels of the peeled tubers and tuberous roots, respectively. High polyamine levels in the surface skin rise to protect the function of polyamines against environmental stresses from the surrounding soil.

The spermidine level (1.50 $\mu\text{mol/g}$ w.w.) and spermine level (0.14 $\mu\text{mol/g}$ w.w.) of the infected potato tuber skins was higher and lower, respectively, than those of the healthy tuber skins (1.00 $\mu\text{mol/g}$ w.w. and 0.16 $\mu\text{mol/g}$ w.w., respectively). However, the spermidine (1.15 $\mu\text{mol/g}$ w.w.) and spermine (0.33 $\mu\text{mol/g}$ w.w.) levels of the peeled tubers in the infected potato were higher than those in the healthy potato (0.85 $\mu\text{mol/g}$ w.w. and 0.12 $\mu\text{mol/g}$ w.w., respectively), suggesting that spermidine level increased in the infected whole tubers and spermine level

increased in the inside of the infected tubers with powdery scab lesions after the infection of *Spongospora subterranea*.

Since a pure culture of a cercozoan *S. subterranea* has never been successfully obtained, polyamines of the protist remain unknown. Putrescine and spermidine were found but tetraamines were not detected in the heterotrophic cercozoa *Cercomonas* and *Massisteria* (Hamana, 2008). Although contamination of putrescine and spermidine from *S. subterranea* was included as a part of the infected tuber skin polyamines, an increase in spermidine level and a decrease in spermine level might have occurred in the infected potato tuber surface in the present study.

This is the first report on the increase of spermidine content caused by powdery scab disease in potato. Increase of spermidine level may be a defensive function against the three different infectious organisms, two kinds of cercozoa and a kind of nematode in *Blossica* and *Solanum* roots or *Solanum* tubers. Although spermine plays a role in salinity and thermal stress response (Yamaguchi et al. 2006, Sagor et al. 2013) in *Arabidopsis thaliana*, spermine level decreased in *Solanales* root-knot galls and tuber-powdery scabs.

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Table 1. Polyamine concentrations in *Solanales* plant organs

Organs of <i>Solanales</i> plants	Polyamines ($\mu\text{mol/g}$ wet weight)										
	Dap	Put	Cad	NSpd	Spd	HSpd	NSpm	TSpm	Spm	AHSpd	Agm
Family Solanaceae											
<i>Solanum lycopersicum</i> (mini-tomato) ('Mini-carol')											
Root-knot gall [3]	ND	0.54 \pm 0.11	0.05 \pm 0.03	ND	1.74 \pm 0.20	0.31 \pm 0.01	0.01 \pm 0.00	0.02 \pm 0.01	0.29 \pm 0.08	0.03 \pm 0.01	0.08 \pm 0.01
Normal root (outside of root-knot galls) [3]	ND	0.35 \pm 0.10	0.05 \pm 0.00	ND	1.37 \pm 0.02	0.62 \pm 0.28	0.01 \pm 0.00	0.05 \pm 0.02	0.71 \pm 0.06	0.18 \pm 0.08	0.07 \pm 0.01
Mature healthy root [2]	ND	0.35	0.02	ND	1.30	0.30	0.01	0.03	0.75	0.06	0.04
Mature crowding hairy root [1]	0.02	0.32	ND	0.02	1.22	0.04	0.30	0.01	0.60	ND	0.02
Young root [1]	ND	0.55	ND	ND	1.32	0.20	ND	0.02	0.85	ND	0.02
Young stem [1]	ND	0.25	ND	ND	1.20	0.02	ND	0.02	0.80	ND	ND
Young leaf [2]	ND	0.35	ND	ND	1.17	0.05	ND	ND	0.50	ND	0.03
Fruit [2]	ND	0.30	ND	ND	0.60	0.04	ND	0.01	0.18	ND	ND
Seed [2]	ND	0.07	ND	ND	1.71	0.02	ND	0.01	0.12	ND	ND
Skin of fruit ('Senka') [3]	ND	0.55 \pm 0.05	ND	ND	1.47 \pm 0.11	0.07 \pm 0.02	ND	ND	0.36 \pm 0.23	0.01 \pm 0.00	ND
Peeled fruit ('Senka') [3]	ND	0.51 \pm 0.02	ND	ND	1.47 \pm 0.21	0.13 \pm 0.02	ND	ND	0.59 \pm 0.18	0.01 \pm 0.00	ND
Seed ('Senka') [1]	ND	0.12	0.02	ND	2.16	0.02	ND	ND	0.02	ND	0.02
<i>Solanum melongena</i> (eggplant) ('Senryo-2')											
Root-knot gall [3]	ND	0.51 \pm 0.03	0.05 \pm 0.01	ND	1.62 \pm 0.03	0.12 \pm 0.04	0.01 \pm 0.00	0.03 \pm 0.02	0.18 \pm 0.07	0.01 \pm 0.00	0.04 \pm 0.01
Normal root (outside of root-knot galls) [3]	ND	0.63 \pm 0.05	0.03 \pm 0.00	ND	1.22 \pm 0.02	0.14 \pm 0.03	0.01 \pm 0.00	0.03 \pm 0.02	0.33 \pm 0.05	0.01 \pm 0.00	0.03 \pm 0.01
Mature healthy root [2]	ND	0.20	0.02	ND	1.25	0.15	0.01	0.03	0.45	0.01	0.03
Young root [1]	ND	0.35	0.03	ND	1.35	0.03	ND	0.01	0.25	ND	0.03
Young stem [1]	ND	0.42	ND	ND	1.21	0.01	0.01	0.08	0.80	ND	0.03
Young leaf [2]	ND	0.70	0.01	ND	1.24	0.02	ND	0.03	0.38	ND	ND
Fruit [2]	ND	0.33	ND	ND	1.15	0.03	ND	0.02	0.50	ND	ND
Seed [2]	ND	0.31	0.04	ND	1.70	0.07	ND	0.05	0.28	0.01	0.01
Skin of fruit ('Kuromasari') [3]	ND	0.37 \pm 0.17	ND	ND	1.23 \pm 0.04	0.06 \pm 0.04	ND	0.01 \pm 0.00	0.30 \pm 0.13	ND	ND
Peeled fruit ('Kuromasari') [3]	ND	0.56 \pm 0.02	ND	ND	1.24 \pm 0.02	0.16 \pm 0.02	ND	0.06 \pm 0.02	0.56 \pm 0.13	ND	ND
Seed ('Kuromasari') [1]	ND	0.25	0.02	ND	2.25	0.06	ND	0.07	0.31	0.01	0.03
<i>Solanum tuberosum</i> (potato) ('Kitaakari')											
Skin of tuber containing powdery scab [3]	ND	0.55 \pm 0.20	ND	ND	1.50 \pm 0.30	0.02 \pm 0.00	ND	ND	0.14 \pm 0.03	ND	ND
Peeled tuber of infected potato [3]	ND	0.39 \pm 0.05	ND	ND	1.15 \pm 0.05	0.03 \pm 0.01	ND	0.01 \pm 0.00	0.33 \pm 0.13	ND	ND
Skin of healthy tuber [3]	ND	0.29 \pm 0.13	ND	ND	1.00 \pm 0.20	0.04 \pm 0.00	ND	0.01 \pm 0.00	0.16 \pm 0.00	ND	0.02 \pm 0.00
Peeled healthy tuber [3]	ND	0.36 \pm 0.04	ND	ND	0.85 \pm 0.15	0.02 \pm 0.00	ND	0.02 \pm 0.01	0.12 \pm 0.04	ND	0.02 \pm 0.00
Bud [2]	ND	0.52	ND	ND	0.80	0.01	ND	0.03	0.64	ND	ND
Stem [2]	ND	0.13	ND	ND	0.93	0.02	ND	0.02	0.67	ND	ND
Leaf [2]	ND	0.31	ND	ND	1.18	0.09	ND	ND	0.71	ND	ND
Fruit [2]	ND	0.35	ND	ND	0.96	0.09	ND	0.01	0.39	0.01	0.03
Tuber ('Beniakari') [1]	ND	0.13	ND	ND	0.59	0.07	ND	0.01	0.25	ND	0.02
Tuber ('Shirowase') [1]	ND	0.30	ND	ND	0.60	0.02	ND	ND	0.21	ND	ND
<i>Capsicum annuum</i> var. <i>grossum</i>											
Fruit (bell pepper, piment) ('Kyunami') [2]	ND	0.60	ND	ND	1.10	0.01	ND	0.01	0.70	ND	0.15
Fruit (sweet pepper) ('Shishitou') [2]	ND	1.00	0.13	ND	0.90	0.01	ND	0.01	0.93	ND	0.02
Family Convolvulaceae											
<i>Ipomoea batatas</i> (sweet potato) ('Beniazuma')											
Skin of tuberous root [3]	ND	1.13 \pm 0.31	ND	ND	1.46 \pm 0.26	0.08 \pm 0.02	ND	0.05 \pm 0.01	1.08 \pm 0.47	0.01 \pm 0.00	ND
Peeled tuberous root [3]	ND	0.55 \pm 0.20	ND	ND	0.81 \pm 0.06	0.04 \pm 0.02	ND	0.03 \pm 0.01	0.80 \pm 0.10	ND	ND
Bud [2]	ND	0.30	ND	ND	1.01	0.03	ND	0.03	1.08	0.02	ND
Stem [2]	ND	0.35	ND	ND	1.15	0.04	ND	0.03	0.83	0.01	ND
Leaf [2]	ND	0.40	ND	ND	1.00	0.08	ND	0.01	1.16	0.01	ND

Dap, diaminopropane [$\text{NH}_2(\text{CH}_2)_3\text{NH}_2$]; Put, putrescine [$\text{NH}_2(\text{CH}_2)_4\text{NH}_2$]; Cad, cadaverine [$\text{NH}_2(\text{CH}_2)_5\text{NH}_2$]; NSpd, norspermidine [$\text{NH}_2(\text{CH}_2)_3\text{NH}(\text{CH}_2)_3\text{NH}_2$]; Spd, spermidine [$\text{NH}_2(\text{CH}_2)_3\text{NH}(\text{CH}_2)_4\text{NH}_2$]; HSpd, homospermidine [$\text{NH}_2(\text{CH}_2)_4\text{NH}(\text{CH}_2)_4\text{NH}_2$]; NSpm, norspermine [$\text{NH}_2(\text{CH}_2)_3\text{NH}(\text{CH}_2)_3\text{NH}(\text{CH}_2)_3\text{NH}_2$]; TSpm, thermospermine [$\text{NH}_2(\text{CH}_2)_3\text{NH}(\text{CH}_2)_3\text{NH}(\text{CH}_2)_4\text{NH}_2$]; Spm, spermine [$\text{NH}_2(\text{CH}_2)_3\text{NH}(\text{CH}_2)_4\text{NH}(\text{CH}_2)_3\text{NH}_2$]; AHSpd, aminopropylhomospermidine [$\text{NH}_2(\text{CH}_2)_3\text{NH}(\text{CH}_2)_4\text{NH}(\text{CH}_2)_4\text{NH}_2$]; Agm, agmatine [$\text{NH}_2\text{C}(\text{NH})\text{NH}(\text{CH}_2)_4\text{NH}_2$]. ND, not detected ($<0.005 \mu\text{mol/g}$ wet weight). Samples were analyzed by HPLC and HPGC, and values were calculated by the combination of the two analyses. (' '), cultivar in Japanese. [], number of samples. Values are shown as M (mean) [2 samples] or M (mean) \pm SD (standard deviation) [3 samples]. This table excluded methylated polyamines found in tomato root and histamine found in potato bud.