Long-term Exposure to Ethylene Affects Polyamine Levels and Sprout Development in ‘Russet Burbank’ and ‘Shepody’ Potatoes

Jin-Cheol Jeong

National Alpine Agricultural Experiment Station, RDA, Pyoungchang, Kangwon 232-950, Korea

Robert K. Prange¹ and Barbara J. Daniels-Lake

Agriculture and Agri-Food Canada, Atlantic Food and Horticulture Research Centre, 32 Main St., Kentville, NS B4N 1J5, Canada

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ABSTRACT. Potato (*Solanum tuberosum* L. ‘Russet Burbank’ and ‘Shepody’) tubers were exposed to continuous $4 \mu\text{L}\cdot\text{L}^{-1}$ ($166 \mu\text{mol}\cdot\text{m}^{-3}$) ethylene in air. Treatment started after 8 weeks in storage and continued up to 33 weeks of storage at 9°C over one (‘Russet Burbank’) or two (‘Shepody’) storage seasons. Tubers were sampled at 3 week (‘Shepody’) or 5 week (‘Russet Burbank’) intervals for polyamine content [putrescine, (PUT); spermidine, (SPD); and spermine, (SPM)] and sprout number and fresh weight per tuber. During the storage period, ‘Shepody’ had higher concentrations of all three polyamines and a higher PUT/(SPD + SPM) ratio, compared with ‘Russet Burbank’. All three polyamines in both cultivars increased during storage, and the increase was more rapid in ‘Shepody’ than in ‘Russet Burbank’. Regardless of cultivar and year, exposure to ethylene induced higher spermidine (SPD) content and a lower PUT/(SPD + SPM) ratio, compared with the air treatment. Sprouts appeared later and were smaller on ethylene-treated tubers and were more numerous in ‘Russet Burbank’. These long-term ethylene effects may be due, in part, to enhanced transformation of PUT to SPD.

The polyamines putrescine (PUT), spermidine (SPD), and spermine (SPM) are found in all living cells and have important growth-regulating properties in plants (Evans and Malmberg, 1989; Galston and Kaur-Sawhney, 1990). During polyamine (PA) biosynthesis, PUT is synthesized from ornithine or arginine via ornithine decarboxylase (ODC) and arginine decarboxylase (ADC), respectively, and is then converted to SPD and SPM (Smith, 1985). S-adenosylmethionine (SAM) participates in the biosynthesis of SPD and SPM, with S-adenosylmethionine decarboxylase (SAMDC) being a key enzyme in this metabolism (Walden et al., 1997). Interestingly, SAM is also the precursor of the plant hormone ethylene which, among other actions, promotes senescence (Adams and Yang, 1977). Although ethylene and PAs have opposite physiological effects, they share SAM as an intermediate in their biosynthesis (Apelbaum et al., 1985; Biondi et al., 1990).

PAs and ethylene may regulate each other’s synthesis, either directly or by metabolic competition for SAM (Evans and Malmberg, 1989). The inhibition of ethylene synthesis by PAs has been studied in a number of plant tissues (Ickson et al., 1986; Kakkar and Rai, 1993; Roberts et al., 1984). Exogenously applied PAs and ethylene inhibit each other’s biosynthesis (Apelbaum et al., 1981, 1982; Ickson et al., 1986). However, they may not compete for SAM. PA and ethylene biosynthetic pathways are not actively competing for the same substrates at any given stage of avocado (*Persea americana* L.) fruit development and ripening (Kushad et al., 1988). In tobacco

(*Nicotiana tabacum* L.) suspension cells, auxin-induced PA accumulation occurs directly, without metabolic competition between ethylene and PA biosynthesis, and indirectly, through auxin-induced ethylene formation (Park and Lee, 1994). In addition, no competition for SAM between PA and ethylene pathways is observed during seedling emergence and establishment of sugar maple (*Acer saccharum* Marshall) (Walker et al., 1989).

Generally, PAs are involved in a variety of growth and developmental processes (Evans and Malmberg, 1989). PAs increase dramatically with the breaking of dormancy in Jerusalem artichoke (*Helianthus tuberosus* L.) (Bagni et al., 1980) and potato (*Solanum tuberosum* L.) tubers (Kaur-Sawhney et al., 1982). Potato seed-tuber age affects PA metabolism in both tuber and shoot tissues (Mikitzel and Knowles, 1989). Transgenic potato plants containing increased sense-SAMDC have higher levels of SAMDC, SPD, and larger numbers of small tubers, compared with control plants (Pedros et al., 1999). Prange et al. (1998) showed that continuous exposure to ethylene over several months delays the appearance of sprouts in ‘Russet Burbank’ tubers; sprouts appear on many eyes but most remain small. These results suggest that there may be a close relationship between ethylene exposure, PA metabolism, and sprout differentiation in potato tubers. PA levels and cell division are positively correlated (Schwartz et al., 1986; Walker et al., 1985). Transformation of PUT to SPD is especially important in the regulation of cell division, e.g., increasing SPD and SPM generally accelerates cell division (Shen and Galston, 1985).

Despite the aforementioned studies on the interaction between ethylene and PAs, little is known about the effect long-term exposure to low concentrations of ethylene on PA metabolism in whole plants. Previous investigations have focused on PA metabolism of in vitro plants exposed to ethylene for short-term periods, e.g., several days. Therefore, the objective of the present study was to determine the effect of continuous long-term exposure to ethylene on PA metabolism, and their possible interaction with sprout differentiation in tubers of two different potato cultivars, ‘Russet Burbank’ and ‘Shepody’.

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¹Corresponding author; e-mail: PrangeR@em.agr.ca.

Materials and Methods

PLANT MATERIAL. Medium-size (≈ 200 g) 'Russet Burbank' and 'Shepody' potato tubers were obtained in October from four growers in New Brunswick and Prince Edward Island, Canada. Six to ten tubers (≈ 1.2 to 2.0 kg) were put into mesh bags and each bag designated a treatment unit.

STORAGE CONDITIONS AND ETHYLENE TREATMENTS. Two experiments were conducted over 2 years (1998–99 and 1999–2000). In the first year, the effect of long-term ethylene exposure on PA metabolism in 'Russet Burbank' (long dormancy) and 'Shepody' (short dormancy) was investigated. For each cultivar, bags of tubers from four separate growers were placed in plastic polyvinyl chloride mesh baskets, with one basket assigned for each grower, and stored in two 0.67-m^3 airtight stainless steel cabinets. All cabinets were ventilated during two 6-h periods per day, interspersed by two 6-h static periods without ventilation. One of the two cabinets for each cultivar was randomly assigned as an air control cabinet while the other was designated as the ethylene-treated chamber. Potato tubers were cured at 13°C for 4 weeks, cooled by 1°C per week for the 4 following weeks, and then stored at 9°C .

The ethylene treatment was applied by addition of ethylene gas to the ventilation air stream after cooling (initial 8 weeks of storage) to maintain a constant ethylene concentration of $4\ \mu\text{L}\cdot\text{L}^{-1}$ ($166\ \mu\text{mol}\cdot\text{m}^{-3}$) in the cabinet, while control potatoes (air) received no additional treatment. In the second year, 'Shepody' potato tubers only were prepared by the same method as mentioned above with the ethylene treatment being applied similarly to the first year.

SPROUT DEVELOPMENT AND FREE PA CONTENT. Sprout development and PA content were evaluated at each removal date (every 3 weeks for 'Shepody' or 5 weeks for 'Russet Burbank') during the storage period. Sprout development was evaluated by determining the number and fresh weight of sprouts (over 2 mm) per tuber.

The methods described by Flores and Galston (1982) and Olson and Nowak (1988) were slightly modified in this experiment to determine free PAs. Samples of tissue (1 cm in diameter, 3 mm thickness) were removed from the apical bud region of tubers. Two grams of chopped tissue was homogenized for 1.5 min in 20 mL of 5% (v/v) cold perchloric acid containing 1,6-diaminohexane as an internal standard and cooled in an ice bath for 1 h. The cooled homogenate was then centrifuged at $25,000\ g_n$ for 20 min. A 2-mL aliquot of supernatant was pipetted into a 15 mL test tube followed by addition of 2 mL $2\ \text{mol}\cdot\text{L}^{-1}$ NaOH and 25 μL of 100% benzoyl chloride. After 45 min at 34°C , 3 mL saturated NaCl and 3 mL anhydrous diethyl ether were added to each test tube, followed by shaking for 2 min. Two milliliters of the ether phase was transferred to another tube, followed by evaporation under nitrogen at 40°C . The residue was dissolved in 400 μL of 100% methanol [high-performance liquid chromatography (HPLC) grade] and filtered through a $0.2\text{-}\mu\text{m}$ filter (Whatman Inc., Clifton, N.J.).

HPLC analysis was performed with a liquid chromatograph (model 1100; Agilent Technologies, Palo Alto, Calif.). The mobile phase consisted of 43 acetonitrile : 57 water (v/v) at a flow rate of $1.0\ \text{mL}\cdot\text{min}^{-1}$. Sample solutions were eluted isocratically

Fig. 1. Changes in the polyamine levels of 'Russet Burbank' (RB, Year 1) and 'Shepody' (Shep, Years 1 and 2) potato tubers as affected by continuous exposure to air or $4\ \mu\text{L}\cdot\text{L}^{-1}$ ethylene during storage at 9°C . (A) Putrescine (PUT), (B) spermidine (SPD), (C) spermine (SPM), and (D) PUT/(SPD + SPM), (Ratio).

at room temperature through a reverse phase C₁₈ ODS analytical (4.6 × 250 mm, 3-μm particle size) and guard column, with PA detection occurring at 245 nm via an ultra violet detector. The PA content of samples was calculated from a standard curve of individual PAs using benzoyl-1,6-diaminohexane as an internal standard.

STATISTICAL ANALYSES. The polyamine data were modeled using a mixed model including the fixed effects: treatment (air and ethylene), time (modeled as a quadratic regression), cultivar and the interaction of these effects; and the random effects: year, cultivar × year × treatment interaction and the cultivar × year × time interaction. This model was fitted using PROC GLM in SAS release 8.01 (SAS Inst. Inc., Cary, N.C.). The residuals were checked, and there was no evidence that the assumptions of analysis of variance (ANOVA) were violated.

To describe the delay in the onset of sprouting the following segmented exponential growth model incorporating a delay parameter was fitted for each chamber using PROC NLIN in SAS release 8.01:

$$y = \begin{cases} 0 & x_i < \delta \\ e^{\beta(x_i - \delta)} - 1 & x_i \geq \delta \end{cases}$$

where y_i represents the average number of sprouts per tuber, x_i represents the time in weeks, β represents the exponential increase parameter, and δ represents the delay parameter. The estimate of the delay parameter was then used as a summary statistic in a two-factor ANOVA [factors: cultivar and treatment (air and ethylene)] fitted using PROC GLM in SAS release 8.01. Unless otherwise noted, results were considered significant if $P \leq 0.05$. The figures were prepared using SigmaPlot software (SPSS, Inc., Richmond, Calif.).

Results

EFFECT OF LONG-TERM ETHYLENE EXPOSURE ON PA CONTENT. ‘Shepody’ tubers, compared with ‘Russet Burbank’, had higher concentrations of PUT, SPD, and SPM. As storage time increased, all three PAs increased in both cultivars, but more in ‘Shepody’ than ‘Russet Burbank’ (cultivar × storage time: PUT, $P < 0.001$; SPD, $P = 0.002$; SPM, $P = 0.010$) (Fig. 1 A–C). The PUT/(SPD + SPM) ratio was higher in ‘Shepody’ than in ‘Russet Burbank’ ($P = 0.019$) (Fig. 1D) and it increased with storage time ($P < 0.001$) without any interaction with cultivar.

Ethylene treatment increased SPD ($P = 0.043$) (Fig. 1B) and this response was not affected by cultivar (treatment × cultivar, $P = 0.208$) or storage time (treatment × storage time, $P = 0.144$). Ethylene treatment decreased the PUT/(SPD + SPM) ratio ($P = 0.024$) (Fig. 1D) and this response was not altered by cultivar (treatment × cultivar, $P < 0.128$) or storage time (treatment × storage time, $P = 0.105$). Ethylene treatment did not influence PUT ($P = 0.114$) (Fig. 1A) or SPM levels ($P = 0.132$) (Fig. 1C).

EFFECT OF LONG-TERM ETHYLENE EXPOSURE ON TUBER SPROUTING. After continuous ethylene treatment started on week 8, the first sprout occurred after 8.7 weeks ± 0.46 (SE) in ‘Shepody’, the short dormancy cultivar, and after 15.0 weeks ± 0.65 in ‘Russet Burbank’, averaged between the two treatments (cultivar, $P = 0.016$). Continuous ethylene exposure delayed the appearance of first sprout by about 5.3 weeks, from 9.2 ± 0.57 (control) to 14.5 ± 0.57 weeks (ethylene) (treatment, $P = 0.017$). The values are the combined data from the two cultivars since this response was not affected by cultivar (treatment × cultivar, $P = 0.269$).

Individual sprout weight and number of sprouts per tuber, measured on the last removal for each cultivar, were both affected

by an interaction between cultivar and treatment ($P < 0.001$) (Table 1). Individual sprout weight on control tubers was lower in ‘Shepody’ than in ‘Russet Burbank’. Ethylene treatment lowered individual sprout weight, more in ‘Russet Burbank’ than in ‘Shepody’.

Sprout number per tuber was low in ‘Russet Burbank’ control tubers and this was increased by ethylene (Table 1). Conversely, sprout number per tuber was high in ‘Shepody’ control tubers and this was not increased by ethylene.

Discussion

It has been suggested that PAs play an important role in the regulation of plant growth and development (Evans and Malmberg, 1989). During the long-term storage of potato seed tubers, the activities of PA biosynthetic enzymes, ODC and SAMDC, increase with progressive sprouting, and the level of PAs in the apical buds increases simultaneously (Kaur-Sawhney et al., 1982). In this study, we observed that PAs increased dramatically in all treatments (Fig. 1). The higher amount of PAs in ‘Shepody’, compared with ‘Russet Burbank’, combined with an earlier and more rapid increase may explain, in part, the shorter dormancy period of ‘Shepody’, compared with ‘Russet Burbank’. A similar trend of PAs with dormancy has also been shown in germinating corn (*Zea mays* L.) seed (Suzuki and Hirasawa, 1980) and Jerusalem artichoke (*Helianthus tuberosus* L.) tubers (Bagni et al., 1980).

Ethylene exposure differentially influences PUT, SPD, and SPM. In deepwater rice (*Oryza sativa* L.), ethylene promotes a significant accumulation of SPD, but PUT increases only slightly (Cohen and Kende, 1986). Park and Lee (1994) reported that ethylene treatment increases the levels of SPD and SPM in suspension cultured cells of tobacco (*Nicotiana tabacum* L.), while PUT is not affected. More recently, Munoz et al. (1999) showed that continuous CO₂ treatment during the storage of cherimoya (*Annona cherimola* Mill.) led to a decline in PUT and a major accumulation of SPD and SPM without any effect on ADC activity. In this study, the long-term exposure of potato tubers to ethylene resulted in a SPD increase (Fig. 1B). These findings agree with some of the reports mentioned above but contrast with data from rice coleoptiles (Lee and Chu, 1992), in which there is a greater accumulation of PUT than SPD and SPM in ethylene-treated coleoptiles. Apelbaum et al. (1985) and Ickson et al. (1985) demonstrated that exposing pea (*Pisum sativum* L.) seedlings to ethylene inhibits the activities of ADC and SAMDC. Thus, the effect of ethylene on PA metabolism may be species specific (Friedman et al., 1989). As for potato tubers, our results showing the induction of a higher SPD and a lower PUT/(SPD + SPM) ratio with continuous exposure to ethylene requires further research to reveal how this induction may occur. Ethylene may be acting directly on critical enzymes, such as SAMDC, or it may be acting first by binding to ethylene binding sites which then induces enzyme up- or down-regulation. Preliminary research with 1-methylcyclopropene (1-MCP), which inhibits the attachment of ethylene to its receptor sites (Sisler and Serek, 1997), suggests that ethylene acts on PAs by first binding to its receptor sites (Prange, Jeong, and Daniels-Lake, unpublished data).

Many investigations have shown there is a close relationship between PA levels and cell division. Walker et al. (1985) demonstrated not only a rapid accumulation of PAs correlates with rapid cell division, but also an inhibition of cell division correlates with the addition of PA biosynthesis inhibitors in sugar maple seed-

Table 1. Effect of continuous 4 $\mu\text{L}\cdot\text{L}^{-1}$ ethylene treatment during long-term storage at 9 °C on tuber sprout weight and number after 33 and 23 weeks of storage of 'Russet Burbank' and 'Shepody' potatoes, respectively. Continuous ethylene treatment was started after the 8th week of storage. The data were transformed to Log₁₀ values for statistical analysis. Each value represents the back transformed mean while the value in parentheses represents the Log₁₀ mean $\pm$ SE.

Cultivar	Treatment	Sprout fresh wt (g/sprout)	Sprouts (no./tuber)
Russet Burbank	Control	4.00 (0.60 $\pm$ 0.13)	3.35 (0.53 $\pm$ 0.08)
	Ethylene	0.03 (-1.49 $\pm$ 0.13)	8.07 (0.91 $\pm$ 0.08)
Shepody	Control	0.69 (-0.16 $\pm$ 0.08)	8.74 (0.94 $\pm$ 0.05)
	Ethylene	0.07 (-1.13 $\pm$ 0.06)	7.22 (0.85 $\pm$ 0.04)

lings. The relationship of PA biosynthesis to cell division also occurs in potato tubers during storage (Kaur-Sawhney et al., 1982), in mung bean [*Vigna radiata* (L.) R. Wilcz.] hypocotyl cuttings during rooting (Friedman et al., 1982), and in apple [*Malus sylvestris* (L.) Mill. var. *domestica* (Borkh.) Mansf.] pollen during tube growth (Bagni et al., 1981). Northcott and Nowak (1988) observed an increase in polyamine concentration when hydrogen cyanamide was applied to potato tubers as a dormancy release agent. The response included more intensive sprouting in the apical eyes. Polyamines are known to affect the synthesis and activity of macromolecules, membrane permeability, and some steps in mitosis and meiosis (Galston and Kaur-Sawhney, 1995). A high PA content has also been linked to the promotion of a wide variety of plant growth and developmental processes (Galston and Kaur-Sawhney, 1995). In particular, the transformation of PUT to SPD increases the cell division rate and a high PUT/(SPD + SPM) ratio is generally correlated with an increased elongation rate. PUT appears to be injurious to, while high SPD (and SPM) seem essential for the G₁ to S transition (Galston and Kaur-Sawhney, 1995). Based on our results, we propose there is a close relationship between the metabolism of PAs and the development of sprouts in potato tubers exposed to ethylene. In particular, our results support the previous suggestion (Galston and Kaur-Sawhney, 1995) that an increase in SPD, and a corresponding decrease in the PUT/(SPD and SPM) ratio, play a key role in this relationship.

In this study, continuous ethylene treatment induced an immediate increase in SPD, but instead of an immediate increase in sprouting there was a delay in both cultivars, as observed previously by Prange et al. (1998) on 'Russet Burbank'. This may be due to the continuous nature of the ethylene treatment. Ryalski et al. (1974) showed that ethylene treatment of nonsprouting tubers shortens the duration of rest markedly, with sprouting being promoted by short (up to 72 h) exposures. The increase in sprouting after ethylene is stopped (Ryalski et al., 1974; Prange, unpublished data) is likely associated with the increased amount of SPD induced by the ethylene. In the same study by Ryalski et al. (1974), inhibition of sprout elongation was observed when sprouting tubers were exposed continuously to ethylene over a 14-d study period. Similarly, in this study and Prange et al. (1998), when the sprouts eventually appear in the ethylene-treated tubers, they may be more numerous, as in 'Russet Burbank'. They are always smaller, have no roots, and tend to abscise more easily. Thus, it seems that the ethylene-induced increase in SPD did not result in earlier and more sprouting because the continuous ethylene treatment induced other ethylene responses resulting in smaller, rootless sprouts and abscission.

In conclusion, we propose that continuous exposure to ethylene favors the transformation of PUT to SPD, and subsequently leads to higher levels of SPD in potato tuber tissue. This increase

in SPD likely promotes cell division in eyes and the development of sprouts, but the continued presence of exogenous ethylene counteracts the growth of these new sprouts, resulting in many uniform but small sprouts.

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