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Polyamine Metabolism of Potato Seed-Tubers During Long-Term Storage and Early Sprout Development[1]

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ABSTRACT

Growth potential of potato (*Solanum tuberosum* L.) plants is influenced by seed-tuber age. After 24 days of growth, single-eye seedcores from 7-month-old seed-tubers produced 64% more foliar dry matter than those from 19-month-old seed-tubers, reflecting a higher growth rate. This study was initiated to determine if differences in polyamine (PA) metabolism are associated with aging and age-reduced vigor of potato seed-tubers. As tubers aged in storage, putrescine (Put) increased 2.2-fold, while spermidine (Spd) and spermine (Spm) decreased 33% and 38%, respectively. Ethylene content of the tuber tissue also increased with advancing age, suggesting that during the aging process *S*-adenosylmethionine was directed toward ethylene biosynthesis at the expense of the PAs. Single-eye cores from 7- and 19-month-old tubers were sown and PA levels in core and shoot tissues were monitored during plant development. Put titer of younger cores increased 8.8-fold by 12 days. In contrast, the increase in Put over the initial titer in older cores was 2.9-fold. The reduced ability of older cores to synthesize Put during plant establishment is probably due to a 45% decline in ornithine decarboxylase activity between 12 and 16 days after planting. Lack of available Put substrate limited the biosynthesis of Spd and Spm, and thus their concentrations remained lower in older cores than in younger cores. Lower PA titer in older cores during plant establishment is thus coincident with reduced growth potential. Concentrations of Put and Spd were higher in shoots developing from older cores throughout the study, but there was no age-related difference in Spm content. In contrast, activities of arginine and *S*-adenosylmethionine decarboxylases were higher in shoots from younger cores during establishment. The results indicate that aging affects PA metabolism in both tuber and developing plant tissues, and this may relate to loss of growth potential with advancing seed-tuber age.

In plants, the amino acids arginine and ornithine provide the main carbon skeletons for synthesis of the PAs[2] Put, Spd, and Spm. The biosynthetic pathway for these PAs is summarized in Figure 1. Interestingly, SAM is a precursor which is shared by both PAs and ethylene. Conversion of SAM to ACC leads to ethylene production, but once SAM is decarboxylated by SAMDC, it is committed to PA synthesis (14). The syntheses of ethylene and PAs are thus interdependently related (26). Though ethylene and PAs share a common intermediate, they have opposite physiological effects: ethylene promotes senescence, while PAs delay senescence (1).

PAs have been reported to have important growth-regulating properties in plants. Kaur-Sawhney *et al.* (17) showed that cells in a rapidly growing phase of development are very rich in PAs. PA titer increased dramatically with the breaking of dormancy in Jerusalem artichoke (*Helianthus tuberosus* L.) tubers (3) and during sprouting of potato tubers (16). Furthermore, increased plant vigor in several species has been directly correlated with high PA titer (25).

The biological activity of PAs is most likely attributed to the cationic nature of the molecules, which facilitates their interaction with cellular anions such as nucleic acids and membrane phospholipids. The mechanism through which PAs influence growth and development is unknown, but they may exert a direct influence on nucleic acid and protein synthesis or on membrane stabilization. For a review of PA metabolism in plants, see (13), (24) and (26).

Sprouting of potato seed-tubers involves an increased rate of nucleic acid and protein synthesis which leads to plant growth and development. Age of the seed-tuber can greatly influence subsequent growth: advanced tuber age (*e.g.* greater than 12 months from harvest) often yields less vigorous plants. Since PAs are known to both stimulate growth and deter senescence, this study was initiated to determine the effect of long-term storage on PA content of potato seed-tubers and also to characterize the effect of tuber age on PA metabolism during sprouting and early plant establishment. In this study, changes in PA content are related to reduced vigor of plants from aged seed-tubers and data are discussed in light of previously published results (18–21).

MATERIALS AND METHODS

Plant Material, Storage, and Culture

Potato (*Solanum tuberosum* L., cv Russet Burbank) seed-tubers (PVX-tested, Elite III) were stored at 4°C (95% RH). Changes in PA titer, as a function of storage duration, were characterized by analyzing cores (1.8 cm diameter) cut longitudinally (apical to basal) from 7, 19 and 31-month-old tubers. Cores from five tubers of each age were collectively sliced, frozen at −20°C and lyophilized. The lyophilized tissue

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[2] Abbreviations: PA, polyamine; Put, putrescine; Spd, spermidine; Spm, spermine; SAM, *S*-adenosylmethionine; ACC, 1-aminocyclopropane-1-carboxylic acid; SAMDC, *S*-adenosylmethionine decarboxylase; PCA, perchloric acid; ADC, arginine decarboxylase; ODC, ornithine decarboxylase.

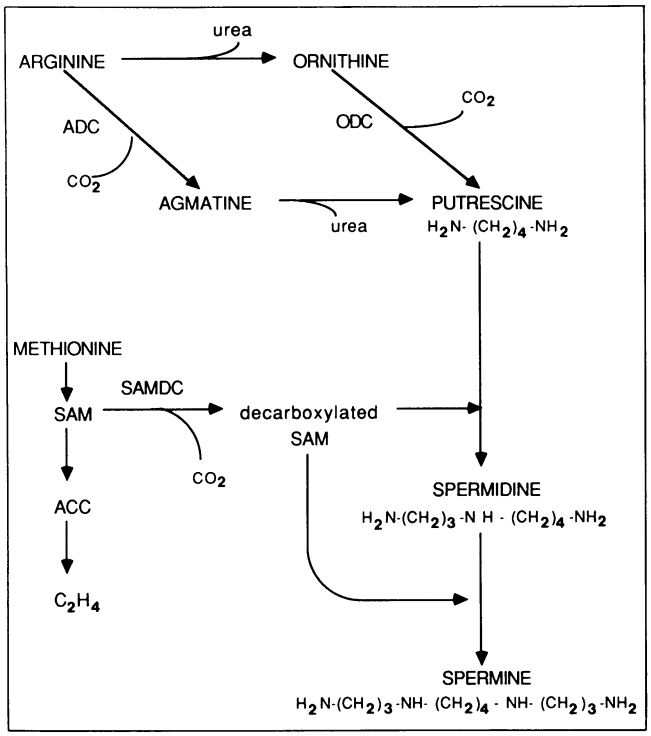

Figure 1. Interrelationship between the ethylene and PA biosynthetic pathway in plants as modified from Galston (13).

was ground in a mortar and pestle and the free PAs were analyzed as described below. There were four replicates of each tuber age (20 tubers analyzed per age).

For plant growth and development studies, 7- and 19-month-old seed-tubers were removed from storage, acclimated to room temperature for 24 h in the dark and blocked for size. Single-eye-containing cores (1.8 cm diameter) were then cut from the middle portion of the tubers perpendicular to the long (apical to basal) axis as previously described (20). A 2 cm long core was cut from both ends of the main cores such that one contained a single-eye (seedcore) and the other only periderm (residual core). Apical and basal cores were avoided. Core fresh weights were recorded, seedcores were planted three per pot and the corresponding three residual cores were sliced thinly, frozen at −20°C and lyophilized for zero-time (at planting) PA determinations.

Seedcores were planted at a depth of 5 cm into 15-cm diameter pots containing a sterile, nutritionally inert medium of peat:vermiculite (1:2, v/v). The pots were placed in a growth chamber with 25/18°C day/night temperatures in a randomized complete block design with four blocks and eight treatments (two seed-tuber ages × four harvest dates). A combination of cool-white fluorescent and incandescent bulbs provided 450 $\mu E\ m^{-2}\ s^{-1}$ light intensity for 16 h per day. Pots were watered as needed and plants were harvested 12, 16, 20 and 24 d after planting. At each harvest, portions of the fresh shoot and seedcore tissues were used to assay activities of the PA biosynthetic enzymes directly. The remaining tissues were frozen at −20°C, lyophilized and used to assay content of the free PAs.

Extraction and Assay of Free PAs

Lyophilized tuber and shoot tissues were ground in a Wiley mill (40 mesh screen). Extraction of free PAs was accomplished by grinding (mortar and pestle) 225 mg of either tissue in 1 mL of 10% (v/v) PCA at 4°C. The crude homogenates were incubated for 1 h on ice, then centrifuged for 15 min at 26,000*g* (4°C). The free PAs within the resulting supernatants were separated by TLC as described below.

Standards, consisting of 1 mM each of Put, Spd and Spm (Sigma), along with the PCA-soluble extracts, were dansylated according to (12), and 20 μL of each extract was loaded on the preadsorbent zone of high resolution silica gel TLC plates (Whatman LK6D). The chromatogram was developed for approximately 1 h in chloroform:triethylamine (25:2, v/v). Following TLC, location of the derivatized PA bands was established in UV light; the PAs were then scraped from the plates, eluted in 2 mL ethyl acetate, and quantified using a Perkin-Elmer fluorescence spectrophotometer (model 650-10LC). Emission at 500 nm was monitored after excitation at 350 nm.

Enzyme Assays

Fresh tuber and shoot tissues were extracted (mortar and pestle) at 4°C in 100 mM phosphate buffer (pH 7.6). The extraction ratio was 5 g tissue/1.5 mL buffer. The homogenate was centrifuged (26,000*g*, 15 min, 4°C) and activities of ADC, ODC, and SAMDC within 100 μL of supernatant were analyzed according to (16). ODC activity was determined by measuring the $^{14}CO_2$ released from the substrate DL-[1-^{14}C] ornithine (49 mCi/mmol; NEN). Similarly, ADC and SAMDC activities were measured using L-[U-^{14}C]arginine (324 mCi/mmol; NEN) and [carboxyl^{14}C]SAM (60 mCi/mmol; NEN). The reaction mixtures contained 10 μL of 20 μCi/mL of each nuclide, diluted with unlabeled L-ornithine, L-arginine, or SAM to yield final concentrations of 66, 9, and 2.7 mM, respectively.

Enzyme assays were carried out in 3.7 mL glass vials fitted with serum stoppers. A filter-paper disc (7 mm diameter), impregnated with 50 μl of 2 N KOH, was suspended inside each vial from the serum stopper to trap the $^{14}CO_2$ liberated. For all three enzyme assays, the reaction mixture (containing 100 μl crude enzyme and 10 μl of the appropriate substrate) was incubated for 45 min at 37°C. The reaction was stopped by injecting 200 μL of 10% (w/v) TCA into each vial. The vials were incubated for an additional 45 min to facilitate quantitative trapping of the $^{14}CO_2$. The filter-paper discs were removed, immersed in 2 mL of ScintiVerse E (Fisher) and the radioactivity liberated was determined by counting in a Packard Minaxi B Tri-Carb 4000 liquid scintillation counter. Enzyme activity was expressed as nmol $^{14}CO_2$ liberated/h·g fresh weight.

Internal Ethylene Extraction and Assay

The internal ethylene concentration of tubers stored 7, 19, and 31 months (4°C, 95% RH) was quantified by GC utilizing a photoionization detector (4). Whole tubers were blocked for size and sliced; internal gases were extracted from the slices

utilizing a vacuum extraction method (6). The method was modified so that the tissue was submersed in a saturated solution of $(Na)_2SO_4$ in the extraction apparatus. This reduced the solubility of ethylene, thus increasing the accuracy of detection (6). The submerged tissue was subjected to a constant vacuum of 200 mm Hg for 2 min. Ethylene content of the extracted gas sample was analyzed with a Photovac model IOA10 portable GC fitted with a photoionization detector (Photovac Inc., Thornhill, Ontario, Canada). A 244 × 3 mm teflon column, containing Carbopack B (60–80 mesh)/1.5% × E-60/1.0% H_3PO_4 (Supelco Canada Ltd), was used with purified air (15 mL/min) as the carrier gas. The GC was run at ambient temperature. Two experiments, each involving three replicates of each age, were performed.

Statistical Procedures

A randomized complete block design was used in each of the studies reported herein. Plant growth, PA titer and PA biosynthetic enzyme activities were subjected to analysis of variance and, where appropriate, sums of squares were partitioned into individual degree-of-freedom components of both main effects and interactions. Based on the results of the analyses of variance, regression analysis was used to derive polynomial models describing the various relationships.

RESULTS

Changes in Tuber PA and Ethylene Content during Storage

The effect of long-term storage on PA content of potato seed-tubers is presented in Figure 2a. As tuber age advanced from 7 to 31 months, significant linear trends in Put, Spd, and Spm content were observed. Put increased 2.2-fold while Spd and Spm decreased 33 and 38%, respectively. In addition, tissue ethylene concentration was found to increase by 60% as tubers aged from 7 to 31 months (Fig. 2b).

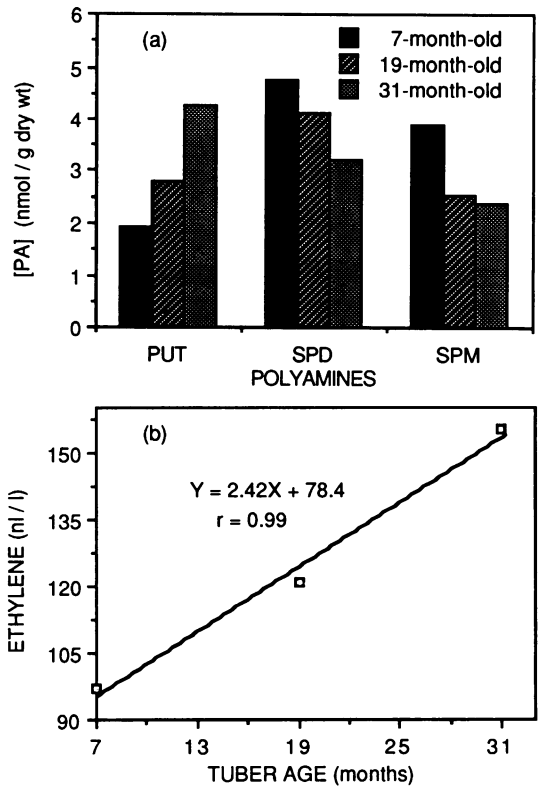

Figure 2. Effect of chronological age on free-PA (a) and internal ethylene content (b) of potato seed-tubers stored at 4°C and 95% RH. *F* values for the linear effect of age on Put, Spm, and ethylene content were significant at the 0.05 level and for Spd at the 0.01 level.

Growth and Development from Aged Seed-Tubers

Single-eye-containing cores from 7- and 19-month-old seed-tubers were sown and plant growth was compared over a 24 d interval. Changes in PA titer and biosynthetic enzyme activities in both seedcore and plant tissues were also followed. Shoot and root dry matter accumulation (mg/core) are shown in Figure 3. The trend in total foliar dry matter (Fig. 3a) from both core ages was quadratic; however, the growth rate of plants from younger cores was significantly greater than that from older cores, reflecting a negative effect of advanced seed-tuber age on plant vigor. After 24 d of growth, 7-month-old cores had produced 64% more foliar dry matter than 19-month-old cores. Similarly, root growth of plants developing from younger cores was 50% greater than that from older cores after 24 d (Fig. 3b). Root growth of plants from younger cores was linear, while that from older cores was quadratic. In addition to the negative effect of advanced seed-tuber age on plant vigor, an influence on the partitioning of plant dry matter is illustrated by the root-to-shoot ratios (Fig. 3b, inset), where a highly significant ($P < 0.01$) age × time interaction was characterized. In 7-month-old seedcores, roots were produced at a faster rate than shoots during the initial stages of establishment, resulting in a root/shoot ratio greater than 1. In contrast, the rate of foliar growth from older seedcores exceeded the rate of root growth throughout the study, as indicated by a root/shoot ratio consistently less than unity. Furthermore, the root/shoot ratio of plants from younger seedcores decreased while that from older seedcores increased over the growth period.

PA Metabolism during Development

Change in Put titer (nmol/g dry weight) of seedcore tissue over the 24 d growth period is shown in Figure 4a. In 7-month-old cores, Put content increased 7-fold, reaching a maximum of 14 nmol/g dry weight by day 14; this was 100% higher than the maximum (7 nmol/g dry weight) reached in older seedcores (an increase of 2.8-fold over the initial Put content). Like Put, seedcore Spd content (Fig. 4b) changed quadratically over the 24 d growth period. In younger cores, Spd content almost doubled during the first 12 d of growth and then decreased through day 24. In older cores, Spd titer decreased slightly over the first 8 d of growth, then slowly increased to a level approximately 21% higher than the initial content at planting. Spm content of 19-month-old cores was significantly lower than that from 7-month-old cores throughout the study. The main effect of time and the age × time

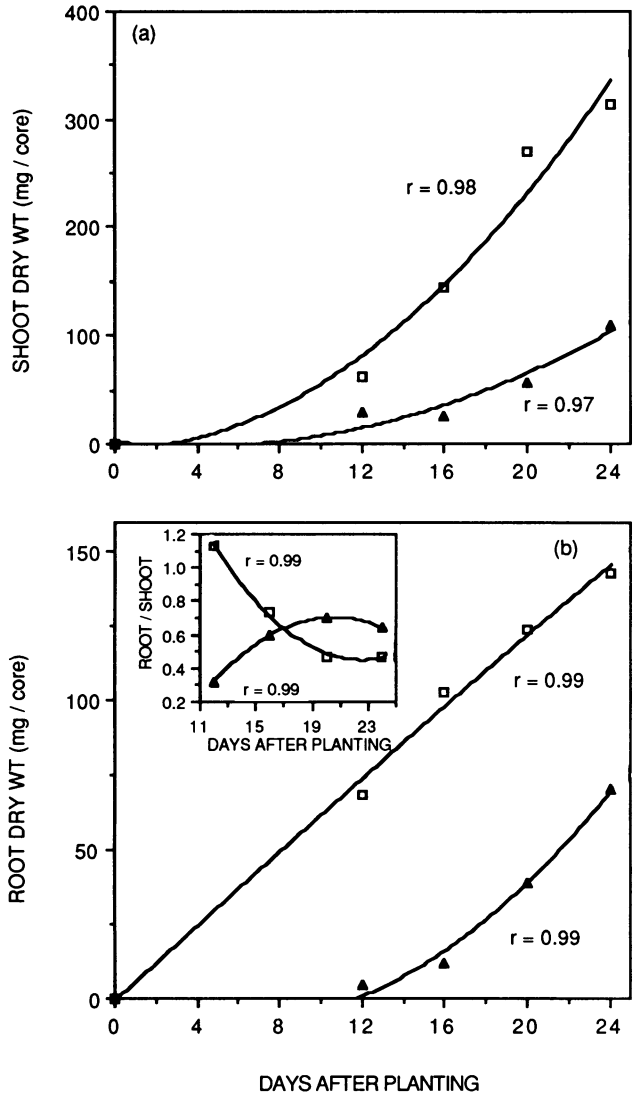

Figure 3. Time course of foliar dry weight (a), root dry weight (b) and root to shoot dry weight ratio (*inset*) from single-eye seedcores from 7- (□) and 19-month-old (▲) seed-tubers. (a) *F* value for the interaction of seedcore age × time (linear) was significant at the 0.01 level. In (b) and *inset*, F values for the interaction of seedcore age × time (linear and quadratic) were significant at the 0.01 level.

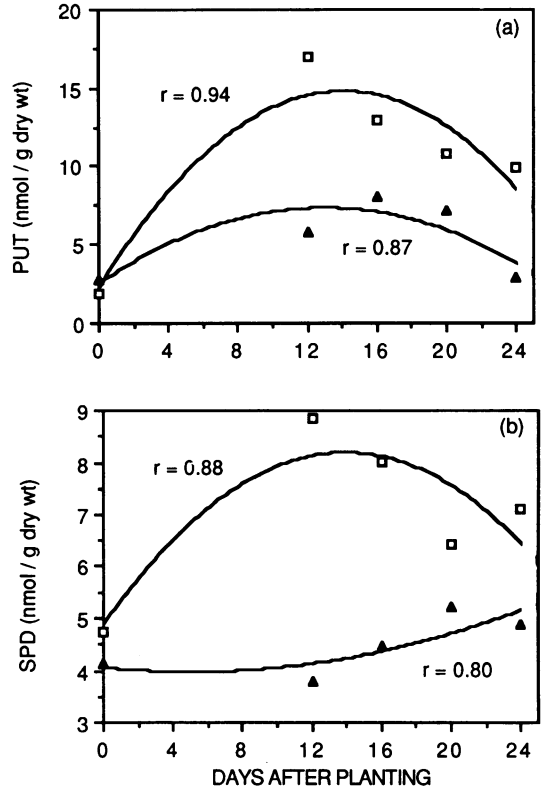

Figure 4. Change in concentration of Put (a) and Spd (b) in single-eye seedcores from 7- (□) and 19-month-old (▲) seed-tubers during plant establishment. *F* values for the interaction of age × time (quadratic) were significant at the 0.01 and 0.10 levels in (a) and (b), respectively. The main effect of seed-tuber age on both PAs was significant at the 0.01 level.

interaction were not significant for seedcore Spm content. The main effect of age, however, was highly significant ($P < 0.01$). Younger seedcores contained 37% more Spm than older cores (3.20 nmol/g dry weight compared with 2.33 nmol/g dry weight) throughout the study.

The activities of the PA biosynthetic enzymes were measured in seedcore tissue at 12 and 16 d after planting (Table I) to coincide with the maximum content of Put and Spd observed in both core ages (Fig. 4). Seedcore age and harvest time had no effect on ADC activity, which averaged 0.14 nmol/h·g fresh weight. From 12 to 16 d after planting, ODC activity decreased 45% in older core tissue. In contrast, the decline in ODC activity from younger core tissue during the same interval was only 6%, illustrating an age × time interaction ($P < 0.10$). Furthermore, SAMDC activity in older seedcore tissue increased 321% from day 12 to 16, while in younger seedcores a 15% decline in activity was evident over the same 4 d interval.

The PA content of shoots developing from 7 and 19-month-old seedcores was measured at 16, 20, and 24 d after planting. The concentrations of Put (Fig. 5a) and Spd (Fig. 5b) were significantly higher in shoots growing from older cores than from younger cores. However, seedcore age had no effect on Spm titer (Fig. 5c). All three PAs decreased linearly with time, and the rate of decrease was not affected by the age of the seed-tubers from which the seedcores were taken. Paradoxically, the activities of the PA biosynthetic enzymes were lower, on average, in shoots from older cores than in those from younger cores (Fig. 6). Arginine decarboxylase activity increased linearly in shoots developing from both seedcore ages; however, the rate of increase was 250% greater in shoots from younger cores than in those from older cores (compare slopes in Fig. 6a). Similarly, SAMDC activity increased linearly in shoots growing from both seedcore ages; however, the rate of increase was equal (compare slopes in Fig. 6b), and shoots from the younger cores had twice the activity of those from the older cores. A significant age × time interaction ($P < 0.01$) characterized ODC activity (Fig. 6c). In shoots growing from older cores, ODC activity increased linearly with time; a quadratic trend characterized ODC activity in shoots growing from younger seedcores.

Table I. *Effect of Seed-Tuber Age on the Activities of ADC, ODC, and SAMDC in Tuber Tissue at 12 and 16 d after Planting*

The reaction mixtures contained 0.1 ml enzyme preparation in 100 mM phosphate buffer (pH 7.6) with the appropriate substrate (see "Materials and Methods"). The reaction mixtures were incubated for 45 min at 37°C and the reactions were stopped by injecting 200 μl of 10% (w/v) TCA into each of the mixtures. The data representing each treatment is the average of 12 seedcores (4 blocks × 3 seedcores per treatment).

Tuber Age	Time after Planting	Decarboxylase Activities		
		ADC	ODC	SAMDC
month	*d*	*nmol $^{14}CO_2$/h·g fresh wt nmol/h· fresh wt*		
7	12	0.11	3.43	6.72
	16	0.13	3.21	5.70
19	12	0.17	4.78	3.45
	16	0.17	2.63	11.09
Age[a]		NS	NS	NS
Time		NS	0.05	0.01
Age × time		NS	0.10	0.01

[a] Indicated sources of variation were either significant at the levels shown or were not significant (NS).

DISCUSSION

As in cut carnation flowers (23) and rice seed (22), aging of potato seed-tubers is accompanied by the accumulation of Put (Fig. 2a). The fact that during long-term storage Spd and Spm titer decreased (while their direct precursor Put increased) suggests less efficient conversion of Put to Spd and Spm with advancing tuber age (Fig. 1). Reduced activity or de novo synthesis of Spd and Spm synthase or limited availability of decarboxylated SAM may be responsible. The increase in ethylene concentration within tubers aged from 7 to 31 months (Fig. 2b) supports the possibility that as potato tubers age, SAM is directed toward ethylene synthesis at the expense of the PA pathway. This would result in a reduction of Spd and Spm levels with a concomitant increase in internal tuber ethylene. Since SAM is a precursor to both ethylene and the tri- and tetra-amines, it appears to be the pivotal point in determining which pathway is completed. Application of exogenous Put or Spd inhibits ethylene production at the SAM to ACC step (11). Furthermore, PA synthesis can be blocked by treatment with ethylene, which inhibits SAMDC (2). In vivo, however, the control mechanism which switches SAM from PA to ethylene production is still unknown. The results lend further support to the idea proposed by Roberts *et al.* (23) that the onset of senescence of plant tissue may be controlled in part by competition between the ethylene and PA biosynthetic pathways for SAM.

In both ages of seedcores, Put and Spd titer increased with sprouting, albeit to a substantially lesser extent in older cores (Fig. 4). During sprouting of seedcores from older tubers, the low levels of Spd and Spm (see "Results") may simply reflect the lower Put content of the cores soon after planting, since Put is a direct precursor of both Spd and Spm.

The reduced ability of older cores to increase their PA titer during plant establishment (Fig. 4) is coincident with reduced growth potential, as characterized in Figure 3. Bagni *et al.* (3)

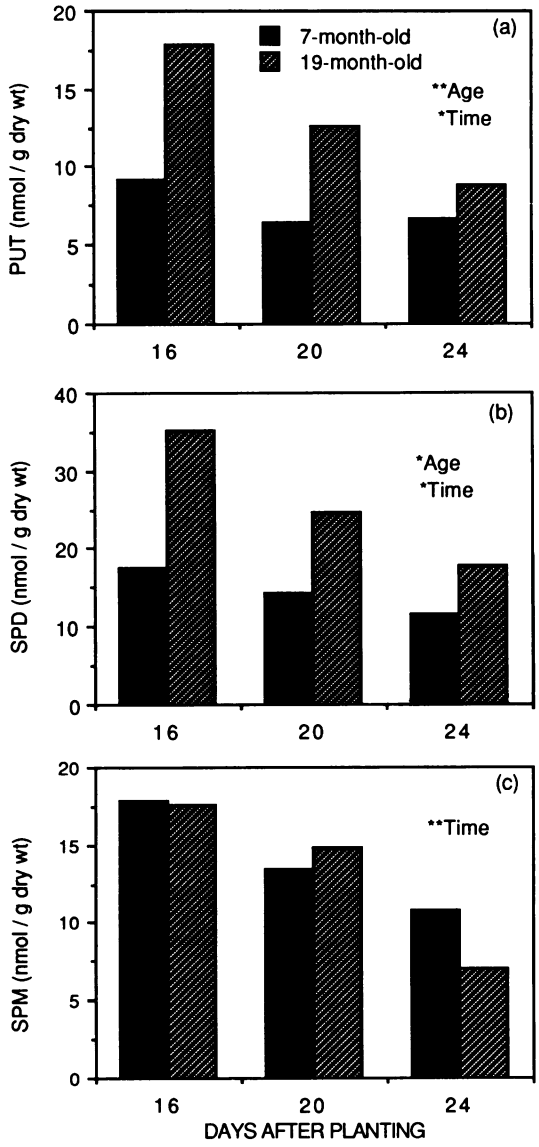

Figure 5. Change in concentration of Put (a), Spd (b), and Spm (c) in foliage developing from single-eye seedcores from 7- and 19-month-old seed-tubers. *,** *F* values for the indicated sources of variation were significant at the 0.05 and 0.01 levels, respectively.

suggested that the increase in PAs with breaking of dormancy in *Helianthus* tubers induced sprouting by stimulating nucleic acid and protein synthesis. On the other hand, Kaur-Sawhney *et al.* (16) attributed second messenger roles to PAs in initiating sprouting of potato tubers. Regardless of the primary mechanism involved, changes in PA titer of seedcore tissue during early plant establishment may relate to the efficiency of mobilization of seedcore carbohydrate and nitrogen reserves to developing sprouts. For example, Srivastava *et al.* (27) found that PAs increased protease activity in the cotyledons of germinating radish seeds by 40 to 50%. They postulated that PAs, by enhancing protease activity, increased reserve protein mobilization and hence growth of the seedlings. Activation of preexisting hydrolytic enzymes or stimulation of the release of proteases were suggested as possible

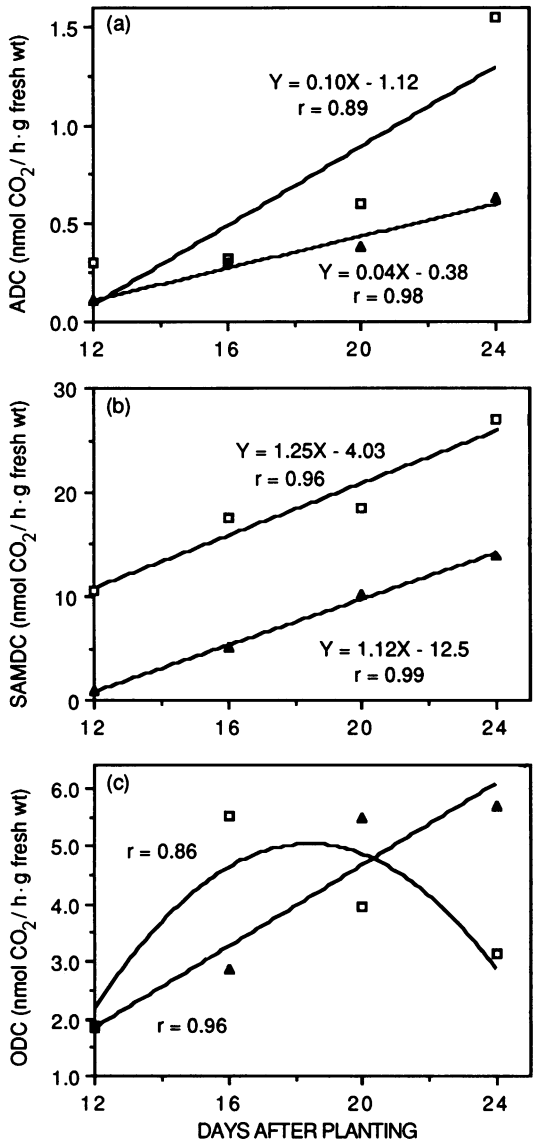

Figure 6. Changes in the activities of ADC (a), SAMDC (b) and ODC (c) of foliage developing from single-eye seedcores from 7- (□) and 19-month-old (▲) seed-tubers. Details of the enzyme assay are the same as in Table I. *F* values for the following sources of variation were significant: (a) age (0.01 level), time linear (0.01) and age × time linear (0.05); (b) age (0.01), time linear (0.01); (c) time linear and quadratic (0.01 and 0.05, respectively) and age × time linear (0.05).

modes of action. Our previous studies have shown that mobilization of tuber carbohydrate and nitrogen reserves is less efficient in tubers aged for 19 months (20, 21). Furthermore, the limitation imposed on plant growth by a lower efficiency of reserve mobilization has been implicated as a contributing factor to age-reduced vigor of potato seed-tubers (20, 21). In 19-month-old potato seedcores, though PA titer does increase marginally with sprouting, mobilization of reserves may be restricted by the lower overall PA content.

Since in seedcore tissue, ADC activity was significantly lower than ODC activity and remained constant during sprouting (independently of seedcore age) (Table I), ADC may not be directly involved in Put synthesis during sprouting. In fact, ODC has been implicated as the rate-limiting enzyme for the synthesis of Put in potatoes (16). At 12 d after planting, ODC activities (Table I) in 7- and 19-month-old seedcores were statistically similar ($LSD_{0.05}$ = 1.54 nmol $^{14}CO_2$/h·g fresh weight). The significant decrease in ODC activity in older cores from d 12 to 16 (Table I) may be responsible for the lower Put content relative to that of younger cores (Fig. 4a).

The dramatic increase in SAMDC activity in older cores may be in response to a lower tissue concentration of Spd and Spm. However, over the 24 d growth period, Spd and Spm titer of older cores never reached the high level evident in younger cores, perhaps because Spd and Spm were rapidly catabolized in the older cores. A more plausible explanation is that the lack of available substrate, namely Put (Fig. 4a), limited the biosynthesis of the tri- and tetra-amines, and thus their concentrations remained lower in older tissue during development. Interestingly, SAMDC is activated by Put in *Vinca rosea* (5) but not in corn (28) or mung bean (9). It is unlikely that SAMDC is a Put-activated enzyme in potato, since in older cores, Put titer was low (Fig. 4a) while SAMDC activity was high (Table I). However, the possibility that SAMDC is stimulated by low levels of Spd or Spm warrants further investigation.

In general, PA titer and activities of the PA biosynthetic enzymes are highest when cell division is most active. This has been shown, for example, in potato tubers emerging from dormancy (16) and in corn root apical meristems (10). Also, Smith and Davies (25) found that PA concentration is directly related to bud size and vigor in peas. Shoots from older seedcores, then, appear to be an anomaly—they have a higher di- and triamine titer with a lower enzyme activity and greatly reduced vigor when compared with shoots from younger seedcores (Fig. 5). Furthermore, the concentration of Spm, which is considered to have a higher growth-stimulating activity than Put or Spd, was equal in shoots developing from the two seedcore ages. Because of a slower rate of sprouting of 19-month-old cores (Fig. 3), the plants produced are developmentally younger than those from 7-month-old cores. In mung bean hypocotyls, higher free polyamine titer is associated with the most actively dividing cells, and bound PAs (TCA-soluble) are associated with the less active, more differentiated cells (15). Since only free PAs were measured in this study, shoots from younger cores, which are developmentally more advanced than shoots from older cores and thus have a higher proportion of more differentiated tissues, may contain less of the free PAs and more of the bound PAs. Conversely, shoots from older cores would have more of the free and less of the bound PAs. It is therefore possible that the less vigorous shoots from older cores do not necessarily contain more total PAs than shoots from younger cores, merely more in the free form as indicated in Figure 5.

In tomato and potato plants, high ODC activity has been correlated with high mitotic division, while ADC has been implicated in cell expansion and differentiation (7). It follows that shoots from younger cores, which are growing at a faster rate than shoots from older cores, should have higher activities of these two enzymes on average. The quadratic trend in ODC

activity in shoots from younger cores may reflect feedback regulation by its product Put (8).

In summary, potato seed-tuber age affects PA metabolism in both tuber and shoot tissues. Over a 31-month storage interval, seed-tuber Spd and Spm titer decreased with a concomitant build-up of Put and tissue ethylene. This would suggest that senescence of potato tubers may be partly controlled by competition between the ethylene and PA biosynthetic pathways for SAM. During plant establishment, ODC activity remained relatively constant in younger seedcores but declined 45% in older seedcores. Hence, Put content of older seedcores remained at a relatively low level during plant establishment and this most likely contributed to the reduced ability of older cores to increase Spd and Spm titer. The resulting low level of PAs in older seed-tubers was coincident with reduced growth potential.

Differences in PA titer and biosynthetic enzyme activities within shoots developing from old and young seed-tubers probably reflect differences in maturity of the developing plants. Although the evidence is largely correlative, it appears that age-reduced vigor of potato seed-tubers may be related to dysfunctions in PA metabolism within the seed-tuber and possibly within the developing plants. The results presented provide a basis for further research on the role of PAs in loss of growth potential during aging of potato seed-tubers.

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