Effect of Potato Seed-Tuber Age on Plant Establishment and Amelioration of Age-Linked Effects with Auxin

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ABSTRACT

Studies were conducted to characterize the effect of advanced potato (Solanum tuberosum L.) seed-tuber age on plant growth potential and whole-plant morphology. Plant growth from single-eye seedcores from 5- to 18-month old 'Russet Burbank' seed-tubers was compared. Loss in apical dominance was apparent with advanced age. On a per-core basis, the amount of plant dry weight was equal for the two ages at 30 days from planting. However, individual plants from older cores displayed reduced shoot, root and leaf dry weights, leaf area, and leaf number. These effects reflected altered dry-matter partitioning and contributed to an overall change in plant morphology with advanced age. On a total seedcore basis, relative growth rate of plants from older seedcores was greater than that from younger seedcores over the 30 day growth interval. Leaf area ratio was also greater for plants from the older seedcores; however, unit leaf rate was not affected by tuber age and plants from both young and old seedcores assimilated dry matter at the same rate. Age-induced differences in growth indices reflected differences in the degree of plant differentiation over the interval of study. Treating younger seedcores with 1-naphthaleneacetic acid (NAA) prior to planting inhibited overall plant growth. In older cores, NAA stimulated root growth, restored apical dominance, decreased leaf number per plant, and increased average leaf area per leaf. In short, NAA altered the morphology of plants growing from older seedcores to more closely resemble that of plants growing from younger seedcores. While auxin significantly altered plant form, vigor of plants from older seedcores was not fully restored by auxin treatment, indicating that age-reduced vigor of potato seed-tubers is not solely mediated by auxin.

Early sprout vigor significantly influences yielding ability of potato (Solanum tuberosum L.) (17). Seed-tuber physiological age, a somewhat subjective measure of the developmental status of a tuber, is a major factor in determining the number and vigor of shoots produced upon sprouting. Indeed, seed-tuber age influences all stages of daughter plant growth, from sprouting to final yield (2, 3, 6, 7). Hence, understanding the processes of aging in potato seed-tubers is of considerable agronomic importance. Storage time and temperature interact to dictate physiological age, which in turn influences the length of the incubation phase of potato seed-tubers. The incubation phase is the period between the onset of sprouting, and tuber initiation on the developing sprouts (12). Even at storage temperatures which are inhibitory to sprouting (below approximately 5°C), tubers which have entered the incubation phase continue to age and sprout growth occurs at a very slow rate (10, 11). The length of the incubation phase is temperature dependent, with low temperatures prolonging it and higher temperatures accelerating it (5). Hence, a given physiological age can be produced by manipulating storage temperature and/or length of the storage period.

Many of the age-induced alterations in potato plant growth appear to be auxin related. For example, treatment of 20-month-old potato seed-tubers with auxin decreased the number of stems produced per seedpiece and increased the average tuber size and total yield (9). With advancing age, the loss in apical dominance is first evident between eyes on the tuber, and eventually multiple sprouts are produced within each eye. Auxin may play a key role in the regulation of apical dominance in many plants (18). Thus, sprouts developing from aged seed-tubers may have a reduced ability to synthesize and/or translocate auxin, or possibly an increased rate of auxin catabolism, resulting in loss of apical dominance and the multiple shoot phenomenon. Reduced ability of plants growing from older seed-tubers to develop roots (13, 14) may be an expression of auxin imbalance, since auxin is involved in root growth and development in many species (18).

Despite several reports on the effects of advanced seed-tuber age on overall growth and yield, an in-depth study characterizing the effect of age on the partitioning of dry matter between plant yield components during early establishment is lacking. Such a study is a prerequisite to defining the mode of action of age-reduced vigor of potato seed-tubers. In this study, we have characterized the way in which advanced seed-tuber age influences growth potential and morphology at the whole-plant level. Furthermore, we have demonstrated that the alterations in plant morphology due to advanced tuber age can be partially overcome by auxin. Dysfunctions in auxin metabolism or action are thus implicated in effecting age-reduced growth potential of potato seed-tubers.

MATERIALS AND METHODS

Tuber Sampling

Potato (Solanum tuberosum 'Russet Burbank') seed-tubers (Elite III) were harvested and stored at 4°C (95% RH) for 5
with tubers. F-values to room containing a water-distilled
18°C to 18 months. These conditions totally inhibited sprouting.
In preparation for growth studies, tubers were acclimated
to room temperature for 24 h in the dark and then blocked
for size. Single-eye seedcores for the various studies were cut
with a cork borer (1.8 cm diameter) from the middle portion
of the tubers, perpendicular to the long (apical to basal) axis
and trimmed to a length of 2 cm. The cores were rinsed in
distilled water prior to planting.

Growth Characterization Study

Seedcores from 6- and 18-month-old seed-tubers were
planted into 15-cm diameter pots (3 seedcores per pot) con-
taining a medium of steam-sterilized soil, peat and sand (2:3:3,
v/v/v). The pots were placed in a growth chamber with 25/18°C
day/night temperatures in a randomized complete block
design with 10 treatments (2 seed-tuber ages x 5 harvest dates)
and 6 blocks. A combination of cool white fluorescent and
incandescent bulbs provided 450 μmol photons m⁻² s⁻¹ light

intensity for 16 h per day. Pots were watered as needed,
fertilized at weekly intervals after emergence (250 ml per pot
of 1 g/L 20-20-20 soluble N/P₂O₅/K₂O fertilizer), and the
time of days to emergence was recorded. Plants were
harvested 10, 15, 20, 25 and 30 DAP. At each harvest, plants
were divided into stems, leaves and roots. Stem number, leaf
number and leaf area were recorded. Plant tissues were dried
separately at 80°C for 72 h and dry weights recorded. RGR
(1/W × dW/dt), ULR (1/LA × dW/dt) and LAR (LA/W)
were also calculated (W = plant dry weight, dW/dt = the
change in plant dry weight per unit time).

Auxin Study

Single-eye seedcores from 5- and 17-month-old seed-tubers
were immersed in a solution of 0.1% (w/v) Tween 20 con-

Abbreviations: DAP, days after planting; RGR, relative growth
rate; ULR, unit leaf rate; LA, leaf area; LAR, leaf area ratio; NAA,
1-naphthaleneacetic acid; PA, polyamine.

Figure 1. Shoot and root growth, and leaf development of individual plants from single-eye seedcores from 6- and 18-month-old potato seed-
tubers. F-values for the age x time interactions were significant at the 0.05 level for (B) and (D, inset) and at the 0.01 level for (A), (C) and (D).
described above. The treated cores were then air-dried for approximately 10 min and planted (3 per pot) into medium in 15-cm diameter pots as described above. The pots were arranged in a randomized complete block design with 8 treatments (2 seed-tuber ages × 4 NAA concentrations) and 6 blocks under the growth conditions already described. The plants received 250 ml of a 1 g/L solution of 20-20-20 soluble N/P2O5/K2O fertilizer weekly, starting 21 DAP. The plants were harvested 32 DAP, and the various yield components were handled as in the “Growth Characterization Study.”

Statistical Procedures

For each study, the plant growth data were subjected to analyses of variance and, where appropriate, sums of squares were partitioned into individual degree-of-freedom components of both main effects and interactions. Regression analysis was used to fit polynomial models to the data.

RESULTS

Growth Characterization Study

In this study, seed-tuber age apparently had no effect on time to emergence, and by 10 DAP 100% emergence was recorded. A single shoot emerged from each 6-month-old seedcore. In contrast, seedcores from 18-month-old seedtubers produced an average of 6 shoots. The data in Figure 1 illustrate, on an individual shoot basis, the influence of tuber age on various plant yield components over a 30-day period. The rates of shoot (Fig. 1A) and root (Fig. 1B) growth were significantly lower from the older seedcores. By the end of the study, each plant from the older cores had accumulated 81% and 79% less shoot and root dry matter, respectively, compared with that from younger cores.

Leaf number (Fig. 1C) increased linearly with time, and an individual shoot from a younger seedcore produced twice as many leaves per day (Y = 0.6X – 1.3) as that from an older seedcore (Y = 0.3X – 1.2). Leaf area per shoot (Fig. 1D) increased for plants from both ages of seedcores; however, after 30 d of growth, leaf area of each shoot from 6-month-old cores was 4.2-fold higher than that of each shoot from 18-month-old seedcores, reflecting a highly significant age × time

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Table I. Growth Analysis of Plants Growing from Single-Eye Seedcores from 6- and 18-Month-Old Potato Seed-Tubers

<table>
<thead>
<tr>
<th>Tuber Age (months)</th>
<th>DAP</th>
<th>ULR (mg/cm²·d)</th>
<th>LAR (cm²/mg)</th>
<th>RGR (g/g·d)</th>
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<tr>
<td></td>
<td>6</td>
<td>18</td>
<td>6</td>
<td>18</td>
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<tr>
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<tr>
<td>15</td>
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<td>0.95</td>
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<tr>
<td>20</td>
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<td>0.64</td>
<td>0.18</td>
<td>0.20</td>
</tr>
<tr>
<td>25</td>
<td>0.52</td>
<td>0.55</td>
<td>0.16</td>
<td>0.19</td>
</tr>
<tr>
<td>30</td>
<td>0.52</td>
<td>0.67</td>
<td>0.09</td>
<td>0.12</td>
</tr>
</tbody>
</table>

Age (A)* NSb   0.01
DAP_LT 0.01     0.01
DAP_OT 0.01     NS
A × DAP_LT NS   0.01
A × DAP_OT NS   NS

* Sources of variation (LT and QT subscripts indicate linear and quadratic trends, respectively). b Significance levels for indicated sources of variation.
interaction. Maximum leaf area was reached at 25 DAP (Fig. 1D, inset), where the area of individual leaves on plants from young cores was 2.9-fold greater than that from old cores.

Leaf/stem dry weight ratio was calculated to assess the effect of tuber age on dry matter partitioning within the shoots. A significant (P < 0.01) age × time (quadratic) interaction in the ratio was characterized (Fig. 2), with a maximum occurring 20 to 23 DAP. At 10 DAP, the leaf/stem dry weight ratio was zero for plants from 18-month-old seedcores, due primarily to emergence and growth of stems in the absence of leaf expansion. However, at its maximum, the ratio was 1.5-fold higher for shoots from younger cores compared with those from older cores.

On a total seedcore basis, the RGR of plants from older cores was significantly greater than that of plants from younger cores, even though ULR, a measure of the efficiency of the plant as a producer of dry matter, was equal for plants from both ages (Table I). Plants from younger cores were initially more efficient at increasing leaf area, as measured by LAR, than plants from older cores. By 15 DAP, LAR was equal for plants from both ages of seedcores and, with further growth, the LAR of plants from older cores surpassed that of plants from younger cores and remained 26% higher for the duration of the study.

The polygonal diagrams of Figure 3 represent, on a total seedcore basis, the influence of seed-tuber age on whole-plant development and morphology. The results of the analysis of variance for each of the yield components displayed in Figure 3 are summarized in Table II. Seed-tuber age significantly affected all parameters measured. The effect of age on apical dominance was evident as early as 10 DAP. Stem dry matter increased linearly for plants from both ages of seedcores, and collectively, the stems from older cores grew 12% faster (P < 0.01) than those from younger cores. Compared with the single stem from 6-month-old seedcores, the multiple stems from 18-month-cores accumulated 80 mg more dry matter by 30 DAP. This is a small but significant difference (Table II).

The increase in leaf number per core was the second age-linked growth effect manifested early in the study (Fig. 3). By 30 DAP, plants from older seedcores averaged a total of 46 leaves compared with 18 for those from younger cores. Similarly, the accumulation of leaf dry matter with time depended upon seedcore age. At all harvest dates, leaf dry weight for plants from older cores was lower than that for plants from younger cores, even though the rate of leaf dry matter accumulation for plants from older cores was 1.8-fold greater (P < 0.01) than that of plants from younger cores over the study interval.

Leaf area per core also increased with time, and significant differences existed between plants from the two ages of seedcores (Fig. 3). Initially (up to 15 DAP), leaf area of plants from younger cores expanded more rapidly, reaching a level 40% greater than that from older cores. By 20 to 25 DAP, leaf area was similar for plants from both ages of seedcores; however, by 30 DAP leaf area of plants from older cores exceeded that from younger cores by 26%. The root growth rate of plants from older cores was 41% greater (P < 0.01) than that from younger cores; yet by 30 DAP, no significant effect of seedcore age on root dry weight was evident.

**Auxin Study**

The potential of auxin to restore apical dominance and plant vigor was studied by pretreating seedcores with NAA. In this study, the rate of plant emergence depended on both seed-tuber age and NAA concentration. Although increasing the concentration of NAA delayed emergence of plants from both ages of seedcores, the effect on younger cores was much
greater than that on older cores. Plants from untreated 5-month-old seedcores achieved 100% emergence by about 10 DAP, 2.5 d later than those from 17-month-old controls. Treating 17-month-old seedcores with 50 and 100 mg/L NAA resulted in 100% emergence by 10 DAP; however, 150 mg/L NAA delayed emergence by an additional 4 d. Treating 5-month-old seedcores with 50 and 100 mg/L NAA increased the time to 100% emergence by 1.9 and 2.4-fold, respectively, compared with controls. By 32 DAP, many of the younger seedcores treated with 150 mg/L NAA had failed to sprout.

Shoot (Fig. 4A) and root dry matter (Fig. 4B) of plants from younger cores were inversely related to NAA concentration. Decreases of 99% and 89% in shoot and root dry matter, respectively, were obtained by treating 5-month-old cores with 150 mg/L NAA. Conversely, dry matter accumulation per shoot from 17-month-old seedcores treated with 50 mg/L NAA was increased by 2.1-fold over the controls, and no additional increase in shoot dry weight occurred with greater NAA concentrations. Root dry matter of plants from 17-month-old cores was also increased maximally (3.2-fold over controls) by treatment with 50 mg/L NAA.

Leaf number per shoot of plants from 5-month-old cores decreased from 11.7 to 1.7 as the concentration of NAA increased from 0 to 150 mg/L (Fig. 4C). In contrast, plants from 17-month-old seedcores averaged 7.8 leaves per shoot and leaf number was unaffected by NAA treatment. Leaf area per shoot from younger cores also decreased linearly with increasing NAA concentration; however, leaf area of shoots from NAA-treated older cores doubled compared with control (Fig. 4D). Similar trends were observed in leaf area per leaf (Fig. 4D, inset).

Leaf/stem dry weight ratio (Fig. 5) for plants from untreated, 17-month-old seedcores was lower than that from 5-month-old untreated seedcores. This trend was also noted at 30 DAP in the Growth Characterization Study (Fig. 3). A linear decrease in the leaf/stem dry weight ratio for plants from younger cores occurred with increasing NAA concentration. In contrast, the leaf/stem dry weight ratio increased by 17% in plants from older cores treated with 50 mg/L NAA, reaching a level that was equal to that of the untreated younger cores.

The polygonal diagrams of Figure 6 illustrate, on a total seedcore basis, the overall effects of tuber age and NAA concentration on plant growth and morphology. A summary of the analysis of variance for each yield component displayed in Figure 6 is presented in Table III. Similarities between the shapes of the diagrams for the control plants in Figure 6 and those displayed at 30 DAP in Figure 3 demonstrate the consistency in the effect of advanced tuber age on plant morphology. Small changes in seed-tuber age (e.g., from 5 to 6 months or 17 to 18 months) have little effect on plant form. Upon sprouting of seedcores, stem and leaf number were the yield components most noticeably altered by seed-tuber age.

With the highest concentration of NAA, the number of stems produced per 5-month-old core was reduced to 0.2, reflecting severe inhibition of sprouting. In the absence of NAA, 17-month-old cores produced an average of 5 stems, and as NAA concentration increased, average stem number decreased to 1.8. Treating 5-month-old seedcores with increasing concentrations of NAA resulted in linear decreases in stem weight, leaf number, leaf dry weight, leaf area and root dry weight. Depending upon the yield component, the maximum inhibition ranged from 89 to 99%. Clearly, exogenous NAA greatly suppressed growth from younger seedcores. With the exception of root dry weight, treatment of 17-month-old cores with NAA also resulted in linear reductions of the same yield components; however, the maximum inhibition was only 40% for stem dry weight, 61% for leaf number, 34% for leaf dry weight and 32% for leaf area. Root dry matter of plants from 17-month-old seedcores increased by 23% in response to NAA treatment. Finally, treatment of older seedcores with NAA altered the morphology of plants to more closely resemble that from untreated 5-month-old seedcores (in Fig. 6, compare the overall shape of the 17-month-old, 150 mg/L NAA polygonal diagram with that for the 5-month-old, 0 mg/L NAA diagram).
the "Growth Characterization Study," plants from 6 and 18-month-old seed-tubers emerged simultaneously. Madec and Perennec (12) showed that desprouting seed-tubers at planting eliminates age-related differences in emergence. Moreover, if different ages of seed-tubers are desprouted and then planted after regrowth has started, differences in emergence will not be evident (3). Since the 6- and 18-month-old tubers used in this study had not sprouted prior to planting, similar emergence rates were expected.

After 30 d of growth, total plant dry matter from the two seedcore ages was equal (Fig. 3). Plants from old cores averaged 6-fold more stems and 3-fold more leaves than those from young cores; however, equivalent increases in total stem and leaf dry weights did not occur. The total plant dry weight from older cores was thus divided among the multiple shoots, and as a result, each individual plant from older seedcores was only one-sixth as vigorous as the single plant from younger seedcores (see Fig. 1). Furthermore, individual plants from the 18-month-old cores were not simply 'miniatures' of those from the 6-month-old cores, as evidenced by dissimilar dry matter partitioning. More dry matter was partitioned into stems of plants from older seedcores compared with those from younger seedcores (Fig. 3). Also, the production of more leaves per older seedcore occurred at the expense of dry matter accumulation per leaf. Plants from old seedcores displayed greatly reduced leaf area per shoot and per leaf (Fig. 1D).

The RGR of plants from both ages of seedcores decreased with time (Table I), due to the increasing amount of nonphotosynthetic plant material accumulating. Individual plants from 6-month-old seedcores had significantly more dry weight than those from 18-month-old seedcores at each harvest date (Fig. 1A). The presence of larger quantities of vascular and structural tissues in the larger plants from younger seedcores no doubt contributed to their lower RGR.

LAR, the ratio of assimilatory material per unit plant material present, was also dependent upon seedcore age (Table I). Initially, plants from younger cores were more efficient at producing leaf area than plants from older cores. This is also shown by the leaf/stem dry weight ratio which was significantly lower for plants from the old seedcores (Fig. 2). Over

Figure 4. Shoot and root growth, and leaf development of individual plants from single-eye seedcores from 5- and 17-month-old potato seed-tubers at 32 DAP. The seedcores were immersed in the appropriate concentration of NAA for 5 min prior to planting. F values for the age x NAA concentration interactions were significant at the 0.05 level for (A) and at the 0.01 level for (B), (C), (D), and (D, inset).
the latter part of the study, leaf area of plants from older cores increased at a greater rate (higher LAR); however, leaf dry weight remained significantly lower compared with that from younger cores over the entire growth period (Fig. 3). Interestingly, ULR was similar throughout the study for plants from both seed-tuber ages (Table I). Plants from both ages of seedcores were therefore equally efficient at producing dry matter, and the apparent increased efficiency with which plants from old seedcores increased their leaf area (measured by LAR) did not translate into increased assimilatory efficiency. In other words, the greater number of leaves on plants from old cores are no more efficient at producing dry matter than the fewer leaves on plants from young cores. Furthermore, each 18-month-old seedcore produced six-fold more stems than each 6-month-old core. ULR for each stem (which represents an individual plant) from the older seedcores was therefore reduced by a proportional amount.

Auxin somewhat negated the age-induced changes in plant morphology and vigor. In the absence of NAA, plants from 17-month-old seedcores emerged earlier than those from 5-month-old seedcores. The 5-month-old tubers were just coming out of dormancy when the study was initiated, resulting in the age-related differences in emergence. NAA apparently altered the natural hormonal balance within the meristems of both ages of tubers, effectively delaying sprout emergence. Plants from older cores treated with 50 and 100 mg/L NAA emerged at the same time as those from untreated younger cores. Hence, exogenous auxin may have been compensating for reduced levels of endogenous auxin in the older meristems. Auxin-treated cores from 5-month-old tubers showed reduced sprouting ability. When treated with 150 mg/L NAA, the younger cores appeared to be in a state closely resembling dormancy, as plant emergence had not occurred by 32 DAP. The exogenous NAA, in combination with endogenous auxin, may have resulted in supra-optimal levels of auxin within the younger meristems. The effect was either to prolong dormancy (16) or to directly inhibit sprout growth (18) to the extent where the seedcores appeared dormant. Roots growing from the seedcore tissue were only observed in younger cores treated with 150 mg/L NAA. Clearly, a hormonal imbalance existed within the treated younger cores which favored root growth over shoot growth.

Apical dominance of older cores was restored with NAA treatment and the vigor of individual plants was increased (Fig. 6). For example, untreated seedcores from 17-month-old tubers produced an average of 5 stems with a total dry weight of 342 mg, or 68 mg per stem. With 150 mg/L NAA
Prior to planting, seedcores were treated with 0, 50, 100 or 150 mg/L NAA. The values represent levels of significance of F values for the indicated sources of variation. Data are presented in Figure 6.

<table>
<thead>
<tr>
<th>Source of Variation</th>
<th>Stem No.</th>
<th>Leaf No.</th>
<th>Dry Weight Stem</th>
<th>Leaf</th>
<th>Root</th>
<th>Leaf Area</th>
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<td>[NAA]LT</td>
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<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
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<td>0.01</td>
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<td>0.08</td>
<td>0.16</td>
<td>0.05</td>
<td>50.2</td>
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</table>

* Abbreviations as in Table I.

treatment, the 1.8 stems produced per 17-month-old seedcore collectively weighed 185 mg, or 103 mg per stem. Hence, even though the collective dry weight of stems produced from the NAA-treated old seedcores decreased, a 51% increase in dry weight per stem was evident. This relationship was also true for leaf dry weight (77% increase per leaf) and leaf area (75% increase per leaf).

Shoot and root dry matter (as well as leaf area per shoot and per leaf) from older cores increased significantly in response to NAA, yet remained substantially lower than that from untreated younger seedcores (Fig. 4). Increased competition between multiple sprouts, together with decreased sink strength of individual sprouts for tuber reserves, have been implicated in contributing to the reduced vigor of individual plants from older seed-tubers (8, 13). Auxin, by affecting apical dominance, decreased the competition between sprouts for tuber reserves. Yet, the increase in sprout vigor was not realized. Even after auxin treatment, shoots from older seedcores were apparently less effective sinks for tuber reserves than those from younger seedcores. Also, increasing the NAA concentration above 50 mg/L did not stimulate any additional growth response (positive or negative) from the older seedcores. Hence, an auxin imbalance is probably not solely responsible for the reduced growth potential of plants from aged seedcores. Age-reduced auxin levels, tissue sensitivity to auxin, and/or age-related metabolic dysfunctions in systems regulated by auxin may limit the response of older cores to auxin treatment.

Partial restoration of vigor to older tubers with auxin treatment may be a reflection of age-induced limitations of the various biochemical processes which interact with auxin during sprouting of the tuber. For example, auxin stimulates both PA and protein synthesis, two processes which are essential for, and correlated with, active plant growth (4). It has been proposed that auxin acts through PAs in promoting growth, since hormone-mediated growth in many plant tissues requires PA synthesis prior to response. In dormant *Helianthus tuberosus* tubers (1) and parthenocarpic tomato ovaries (15), auxin-induced growth is preceded by PA biosynthesis and is greatly reduced by inhibitors of the PA biosynthetic enzymes. Recently, reduced vigor of plants from aged potato seed-tubers was correlated with significant reductions in ornithine decarboxylase (the enzyme involved in the first step of PA synthesis) activity and ability to increase putrescine titer of the tuber tissue during sprouting (14). PA biosynthesis was suppressed during sprouting of older tubers, but was not totally dysfunctional. Since auxin treatment of older seedcores only partially restored vigor, the less than maximal response may be due to age-related alterations in the PA metabolic pathway. The possible relationships between PAs, auxin, potato tuber age and sprout vigor warrant further investigation.

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**LITERATURE CITED**

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