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Optimizing Tuber Set and Size Distribution for Potato Seed (*Solanum tuberosum* L.) Expressing Varying Degrees of Apical Dominance

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Abstract Plant emergence, apical dominance, tuber set, and size are affected by the physiological age of seed tubers, which can substantially impact overall crop value. This study investigated the efficacy of seed spacing (15, 25, and 35 cm) and 1-naphthaleneacetic acid (NAA) seed treatments in altering these variables in cv. Ranger Russet to improve yield and tuber size distribution of seed expressing low (2.8 stems/seed piece) and high (4.8–5.4 stems/seed piece) apical dominance. Age primed, high-stem seed produced more tubers per plant and per ha than non-aged seed; however, tuber number per ha from both seed lots fell to the same extent with decreasing plant density. Importantly, tuber set per plant increased substantially more for the physiologically older, high-stem seed as plant spacing increased. Average tuber weight also increased with decreasing plant density but the response was greatest for the physiologically younger, low-stem seed. Regardless of seed age, marketable yields were comparable at 25- and 35-cm spacing. Tuber size distributions from the 2.8-stem seed shifted from oversize (>340-g) tubers to higher percentage 113–284-g tubers as spacing decreased from 35 to 15 cm. The 5.4-stem seed produced less undersize (<113 g) tubers and a greater proportion of >284-g tubers when planted at 35-cm spacing. Adjusting in-row spacing relative to seed age and expected stem numbers improved tuber size distribution and value. However, because plants from older seed set more tubers in response to decreasing plant density than younger seed, average tuber weight and size distribution never matched the younger seed at any spacing. Restoration of apical dominance by treatment of seed with NAA was more effective in this regard. Depending on seed age, NAA delayed plant emergence (22–74 %) and decreased stem (24–38 %) and tuber numbers per plant (8–13 %). Stem numbers from age-primed seed fell from 4.8 to 3.0 as NAA concentration increased. Marketable yields were not affected by seed age but decreased slightly (7.3 %, $P < 0.01$) with increasing NAA concentration. NAA effectively shifted the tuber size distribution from age-primed seed toward larger (>284-g) tubers, resulting in a yield profile approaching that of the non-treated younger seed. Although seed spacing and NAA treatments are effective techniques for altering tuber size distribution to maximize crop value in relation to seed age and expected stem numbers, tuber age had a small but residual effect on productivity beyond that attributable to apical dominance.

Keywords Auxin · Naphthaleneacetic acid · NAA · Seed age · Stem number · Tuber number · Size distribution

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Introduction

Seed tuber physiological age affects apical dominance and the number of main stems produced per seed piece or whole seed tuber (Krijthe 1962; Iritani and Thornton 1984). Apical dominance decreases with advancing tuber age (Eshel and Teper-Bamnolker 2012), which in turn affects the number of tubers per hill (plant) and ultimately tuber size distribution in a cultivar-dependent but predictable manner (Knowles and Knowles 2006). In general, higher stem numbers result in more tubers per plant and smaller average tuber size (Iritani and others 1983). Age-induced shifts in tuber size distribution often occur with no effect on total yield; however, this depends on cultivar, length of growing season and the extent of aging (Knowles and Botar 1992; Knowles and Knowles 2006). Managing stem numbers by manipulating seed physiological age, therefore, is a recognized strategy to maximize crop value in relation to market requirements for tuber size (Struik and others 1990; Knowles and Knowles 2006; Struik 2007a). Planting aged seed can either enhance or diminish crop value, depending on the end-use requirements for tuber size.

The expression of apical dominance can be effectively manipulated by adjusting seed storage temperatures to either slow or hasten the aging process (Knowles and Botar 1991, 1992; Knowles and Knowles 2006) and/or by treating seed with plant growth regulators prior to planting (Mikitzel 1993; Knowles and others 2005; Blauer and others 2013a). High temperature, age-priming treatments accelerate aging by increasing the basal respiration rate of tubers, leading to earlier dormancy break, decreased apical dominance, more stems, more tubers per plant, and shift in tuber size distribution toward smaller tubers (Blauer and others 2013b). The degree of apical dominance (that is, stem numbers) is thus a good indicator of seed physiological age (Eshel and Teper-Bamnolker 2012).

The mechanism of apical dominance is complex and not fully understood despite more than 80 years of research. Coordinate changes in auxin, strigolactones, cytokinins (Young and others 2014 and references therein), sugar demand by the apical bud (Mason and others 2014) and programmed cell death (Teper-Bamnolker and others 2012) have a role in regulating apical dominance. Treating tubers with auxin inhibits sprout growth (Suttle 2003) resulting in delayed emergence, but increases apical dominance (Knowles and others 1985; Mikitzel and Knowles 1990; Kumar and Knowles 1993). However, the extent of sprout growth inhibition and delayed emergence depend on tuber physiological age and the concentration of auxin. Sprouts developing from older tubers expressing low or no apical dominance have high IAA oxidase activity and reduced ability for polar translocation of native auxin (IAA), which partly accounts for the loss of apical dominance (Kumar and Knowles 1993). Naphthaleneacetic acid (NAA) is not subject to catabolism by IAA oxidase/peroxidase (Goldschmidt and others 1967; Gianfangna 1987) and is therefore more effective than IAA in restoring apical dominance to aged seed tubers (Kumar and Knowles 1993).

The chronological age of seed used commercially is usually constant within a production region. Seed physiological age, however, can vary among seed lots of the same chronological age and is influenced by in-season management, stresses (for example, heat stress) during production, tuber maturation at season end, and storage management (Struik 2007a). Knowing the degree of apical dominance (that is, approximate physiological age) of a seed lot prior to planting would facilitate implementation of management techniques (for example, use of growth regulators and/or cultural practices) to optimize tuber size distribution and maximize crop value. For example, GA application to physiologically young and highly apically dominant seed can effectively hasten plant establishment, increase stem and tuber numbers and decrease average tuber size (Mikitzel 1993; Blauer and others 2013a). Conversely, physiologically older seed expressing low apical dominance can be treated with auxin prior to planting to decrease stem numbers and tuber set, resulting in larger tubers at harvest (Knowles and others 1985). Altering plant population by varying in-row spacing of seed also significantly affects tuber size (Love and Thompson-Johns 1999; Arsenault and others 2001; Bussan and others 2007; Bohl and others 2011) and provides an alternative approach to plant growth regulators for modifying the size distribution of tubers from seed lots expressing varying degrees of apical dominance.

The extent to which age-dependent tuber size distribution phenotypes can be manipulated through such management is not known. Accordingly, we evaluated the efficacy of in-row spacing and NAA treatments as techniques to manipulate tuber size distributions from young and old seed. In particular, we tested the hypothesis that the tuber size distribution phenotype produced by a physiologically older seed lot expressing low apical dominance could be effectively altered to equal that of a younger seed lot expressing high apical dominance by adjusting the in-row spacing of seed or by treating the seed with auxin (NAA) to restore apical dominance. In the latter case, if the effects of seed age on tuber size distribution are manifested solely by higher stem numbers (that is, no other residual influence of seed age), then restoration of apical dominance should translate into a tuber size distribution phenotype comparable to that produced by younger seed. The effects of seed age, spacing and auxin treatments on crop values were also compared.

Materials and Methods

Plant Material

The mainstay cultivar, Ranger Russet, was used for all studies reported herein. This cultivar was released from the Northwest Variety Development Program (U.S.D.A. and Agricultural Experiment Stations of WA, ID, OR, and CO) in 1991 as a late maturing, long russet potato for fresh and frozen process (French fry) markets (Pavek and others 1992). In 2014, cv. Ranger Russet ranked as the second most widely grown potato variety in the U.S. (NASS 2014). The sensitivity of this cultivar to age-priming treatments designed to decrease apical dominance, range of stem numbers, and associated changes in tuber set, average tuber weight and yield with increasing stem number are similar to cv. Russet Burbank (Knowles and Knowles 2006; Blauer and others 2013b).

The relative growth responses and productivities of age-primed versus non-age-primed 'Ranger Russet' seed tubers to in-row spacing and seed treatment with 1-NAA were compared in separate field trials (3 years per trial) in the Columbia Basin of Washington over a 6-year period from 2004 to 2009. Seed tubers (G3, certified generation 3 from nuclear stock) were obtained directly from commercial seed growers within one week of harvest (early to mid-October) each year preceding field studies. The seed tubers were stored in the postharvest facilities at Washington State University, Pullman, WA where age-priming treatments were applied.

Age-Priming Treatments

Age-priming seed by storing for brief periods at 32 °C at the beginning of storage (while seed is dormant) is more effective at decreasing apical dominance than treatments given at the end of storage just prior to planting (Blauer and others 2013b). Accordingly, all seed tubers received an initial 80-degree-days (DD) (4 °C base) at 12 °C (10 days at 12 °C) to facilitate wound healing at the start of storage. Seed ages were calculated by summing daily heat units (average temperature minus 4 °C base temperature) to arrive at the accumulated storage degree days (Knowles and Knowles 2006). Half the tubers were then given an additional age-priming treatment by storing at 32 °C (Blauer and others 2013b) for a total of 720 DD (spacing studies) or 600 DD (NAA studies) and then held at 4 °C until planting (ca. 195-day total storage period). The objective of these age-priming treatments was to reduce apical dominance without affecting total yield. Because the 720-DD treatment had a small negative effect (−3.7 %) on total yield in the spacing studies, the duration of heat-priming was reduced by approximately 3 days, resulting in 600-DD seed for the NAA studies. This latter age substantially decreased apical dominance without affecting total yield (see "Results" section). Control (80 DD) tubers were held continuously at 4 °C following the wound healing period. Relative humidity was at least 95 % during storage at all temperatures. Although sprouting of seed was minimal at planting, on average, the 80-, 720-, and 600-DD age-priming treatments resulted in 2.8 ± 0.2, 5.4 ± 0.2, and 4.8 ± 0.4 above ground stems per seed piece, respectively, at 55–62 DAP. These treatments are henceforth referred to by their respective stem numbers (degree of apical dominance) for the spacing studies and by their cumulative degree days (80 vs 600 DD) for the NAA studies.

Field Plot Design, Establishment and Maintenance

Field studies to assess the effects of seed age, in-row seed spacing and NAA on plant emergence, main stem numbers, tuber set, yield, and tuber size distribution were conducted at the Washington State University Research and Extension unit, Othello, WA (46°47.277′N. Lat., 119°2.680′W. Long.). Treatments for seed age and spacing (2 ages × 3 in-row spacings) or seed age and NAA (2 ages × 4 NAA concentrations) studies were factorially arranged in separate randomized complete block designs in field plots with five replicates. Approximately 5 days before planting, 115–200-g seed tubers were hand cut into 50–64-g seed pieces. The field plots were blocked for seed tuber size, number of cut surfaces on the seed piece and seed piece portion (that is, seed pieces derived from apical or basal ends of the seed tubers). Cut seed pieces were held at 9 ± 0.5 °C (95 % RH) until planting, which occurred approximately April 15–19 depending on year.

For spacing studies, seed pieces were hand planted 20-cm-deep and 15, 25, or 35 cm apart in a Shano silt loam soil (Lenfesty 1967) within 6-m-long treatment plots. Individual treatment plots thus contained 40, 24 or 17 plants (seed pieces) per plot, respectively. All plots were flanked by guard rows planted at 25-cm spacing with non-age-primed seed. Rows were 86 cm apart and a 1.3-m alley was left between plots. Guard seed pieces (cvs Dark Red Norland, Chieftain or All Blue) were planted at the beginning and end of each plot to minimize the variation in interplant competition for plants at the ends of plots, and to enable the separation of individual plots during mechanical harvesting in the fall. Plots were situated under a linear move irrigation system. Soil moisture was maintained at a minimum of 65 % of field capacity with the aid of soil tensiometers positioned throughout the field. Preplant and in-season fertilizer applications were based on soil tests and petiole analyses, respectively, following standard practices for late-season russet potatoes in the Columbia Basin. Herbicides, insecticides, and fungicides were applied according to standard practices.

NAA studies were conducted at 25-cm in-row seed spacing (24 seed pieces per plot) essentially as described above. 1-NAA (Sigma-Aldrich, St. Louis, MO) treatment solutions (0, 33, 67, and 100 mg L^{-1}) were prepared in water containing 0.1 % (w/v) Tween 20 from a 50 mg mL^{-1} stock solution of 97 % (w/v) NAA in DMSO. The DMSO concentration was maintained at 0.1 % (v/v) for all treatments, including control (0 mg L^{-1} NAA).

Seed pieces of both ages were rinsed of surface soil and immersed in NAA solutions for 5 min. After drying for about 3 h at room temperature, the treated seed pieces were stored at 9 °C (95 % RH) until planting 3–4 days later as described above. Treatment rows were flanked by guard rows planted with non-age-primed, non-NAA-treated 'Ranger Russet' seed.

Plant Emergence, Stem Counts, Harvesting, and Sorting

Plant emergence counts for all plots in the NAA study commenced about 23 days after planting (DAP) and continued every 2–3 days until all plots reached 100 %. Plant emergence was not recorded for the spacing study. Above ground main stems were counted prior to row closure (55–62 DAP) in all years. Vines were mechanically cut 153–155 DAP and all plots were harvested with a single-row mechanical harvester approximately 2 weeks later. The tubers were washed, weighed, counted and sorted into the following categories: under 113, 113–170, 171–284, 285–340, 341–397 g, over 397 g, and cull tubers. Total yield included the combined weights of all categories. U.S. No. 1 yield was equal to the sum of all categories except cull and undersize (<113-g) tubers, and marketable yield included U.S. No. 1 plus undersize tubers.

Data Analysis and Presentation

For spacing studies, seed from two sources were each subjected to the six age × spacing treatments for 2 years and one seed source was used in year three. Only one seed source was used each year for the NAA studies. Treatment effects were similar from year to year and not affected by seed source. The data presented are therefore averages of five and three seed source years for the spacing and NAA studies, respectively. Growth and yield data were subjected to analysis of variance (ANOVA) with single degree-of-freedom contrasts for main effects (age, spacing, NAA concentration) and interactions, including polynomial trends (linear, quadratic). Where appropriate, coefficients of determination are reported along with significance levels (P values) for correlation coefficients. LSD ($P < 0.05$) values are given for mean separation. Selected growth and yield data are plotted versus NAA concentration ± SE. The effects of seed spacing and NAA on tuber size distributions are presented in polygonal plots of the yields of six tuber size classes expressed as a percentage of total marketable yields.

Economic Analyses

Estimates of the effects of treatments on crop value were derived using mock frozen process contracts ($132 MT^{-1} base price) as defined in Pavek and Knowles (2009). Gross values were calculated based on contract prices in effect for producers in the Columbia Basin of Washington, incorporating incentive/disincentive clauses for premium, undersize and oversize tubers (Pavek and Knowles 2009). Crop value estimates were based solely on tuber size distribution for direct-to-processor delivery. Specific gravity clauses were not considered, nor were premiums or penalties for bruise, tuber fry color, sugar content, or internal defects. The value of tubers as certified (G3) seed was calculated at $198 per metric ton of 57–340-g tubers. Seed costs were subtracted to facilitate comparison of net values at the different planting densities. Costs associated with seed cutting, shipping and NAA treatment were not included in estimates of overall crop value. Economic data are presented as percentage increase or decrease in crop values relative to 25-cm spacing (standard practice) or non-NAA-treated 80-DD (young) seed, depending on the study.

Results

In-Row Spacing Studies

In-row spacing had no appreciable effect on the expression of apical dominance by age-primed (720 DD) and control (80 DD) seed, which averaged 5.4 and 2.8 stems per seed piece, respectively, over the range of planting densities (Table 1). However, the number of tubers per plant from the high-stem seed lot increased 74 % as spacing widened from 15 to 35 cm, compared with 46 % increase from the low-stem seed lot, revealing greater propensity of plants from physiologically older seed to increase tuber set in response to decreasing plant density. Consistent with the increased number of tubers per plant, age-primed seed averaged 45 % more tubers per hectare than non-aged seed and the decrease in tuber number per hectare with wider spacing was equal for both seed lots. The increases in average tuber fresh weight as spacing increased from 15 to 35 cm were 38 % for the low-stem seed and 26 % for the high-stem seed. Plants from the 5.4-stem seed at 35-cm spacing thus yielded 13 % smaller tubers than plants from the 2.8-stem seed at 15 cm spacing, due in large part to the enhanced tuber set response of plants from older tubers with increasing spacing.

The yield of the 2.8-stem seed surpassed that of the 5.4-stem seed by 8.1 MT ha^{-1} (7 %) when spaced at 15 cm, but total yields of the two seed lots were equal at 25 and 35-cm spacings (Table 2). Total yields decreased linearly by 7.7 (2.8-stem seed, $R^2 = 0.99$) and 4.0 MT ha^{-1} (5.4-stem seed, $R^2 = 0.96$) for every 10-cm increase in seed spacing. Excluding undersize (<113-g) tubers, U.S. No. 1 yields also decreased linearly with increasing spacing for

Table 1 Effects of in-row spacing on stem numbers, tuber set and average tuber size from cv. Ranger Russet seed lots expressing high (2.8 stems) and low (5.4 stems) apical dominance

Spacing (cm)	Seed							
	Seed lot (stems plant^{-1})		Seed lot (tubers plant^{-1})		Seed lot (tubers ha^{-1a})		Seed lot (g tuber^{-1})	
	2.8-stem	5.4-stem	2.8-stem	5.4-stem	2.8-stem	5.4-stem	2.8-stem	5.4-stem
15	2.7	5.0	7.0	9.3	530	707	208	145
25	2.8	5.6	8.9	13.3	407	607	251	166
35	2.9	5.5	10.2	16.2	329	524	287	182
$LSD_{0.05}$	0.53		0.6		27		10	
Stem no.[b]	0.01[c]		0.01		0.01		0.01	
$Spacing_{LT}$	NS		0.01		0.01		0.01	
$Spacing_{dev}$	NS		0.05		NS		NS	
Stem no. × $spacing_{LT}$	NS		0.01		NS		0.01	
Stem no. × $spacing_{dev}$	NS		NS		NS		NS	

The 2.8- and 5.4-stem seed treatments were produced by storing seed at 12 and 32 °C for various periods immediately after harvest to accumulate 80- and 720-degree-days, respectively (4 °C base). The seed was then held at 4 °C for the remainder of storage (ca 195 days total). Data are averaged over three growing seasons with two seed sources in years one and two and one seed source in year three (five seed-source years represented)

NS not significant

[a] 1000s

[b] Sources of variation; LT, linear trend; dev, deviation from linearity

[c] Significance levels for the various sources of variation ($P < 0.01$ or 0.05)

Table 2 Tuber yields and size distributions produced by cv. Ranger Russet seed lots expressing high (2.8 stems) and low (5.4 stems) apical dominance

Seed lot	Seed Spacing (cm)	Tuber yields (MT ha^{-1})								
		Total	U.S. No. 1	<113 g	113–170 g	170–284 g	284–340 g	340–397 g	>397 g	Mkt Yld[a]
2.8-stem	15	111.7	100.0	9.7	16.4	39.5	14.8	9.6	19.8	109.6
	25	104.0	95.7	5.8	10.2	27.8	13.6	12.1	32.1	101.6
	35	96.4	90.1	3.8	6.7	21.2	11.3	11.7	39.2	93.9
5.4-stem	15	103.6	77.8	24.0	26.7	34.5	7.4	4.1	5.2	102.0
	25	101.1	83.0	16.6	23.5	36.5	9.6	5.7	7.6	99.5
	35	95.7	80.9	12.9	18.7	33.2	10.9	7.0	11.0	93.9
$LSD_{0.05}$		5.1	5.8	2.0	1.9	4.0	2.4	1.8	4.4	5.1
Stem no.[b]		0.05[c]	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.05
$Spacing_{LT}$		0.01	NS	0.01	0.01	0.01	NS	0.01	0.01	0.01
$Spacing_{dev}$		NS	NS	0.05	NS	NS	NS	NS	NS	NS
Stem no. × $spacing_{LT}$		0.05	0.01	0.01	NS	0.01	0.01	NS	0.01	0.05
Stem no. × $spacing_{dev}$		NS	NS	NS	NS	0.05	NS	NS	NS	NS

The 2.8- and 5.4-stem seed treatments were produced by storing seed at 12 and 32 °C for various periods immediately after harvest to accumulate 80- and 720-degree-days, respectively (4 °C base). The seed was then held at 4 °C for the remainder of storage (ca 195 days total). Data are averaged over three growing seasons with two seed sources in years one and two and one seed source in year three (five seed-source years represented)

NS not significant

[a] Market (Mkt) yield includes U.S. No. 1 yield plus yield of <113-g tubers

[b] Sources of variation; LT, linear trend; dev, deviation from linearity

[c] Significance levels for the various sources of variation ($P < 0.01$ or 0.05)

the 2.8-stem seed lot, but remained constant across spacings for the 5.4-stem seed lot. Trends in marketable yields (U.S. No. 1 + <113-g tubers) with seed age and planting density were the same as total yields. On average, age-primed seed produced substantially higher yields of smaller tubers (<284 g) and lower yields of larger (>284 g) tubers than the 2.8-stem seed. Yields of the four smallest tuber size grades from the 2.8-stem seed decreased with increasing plant spacing while yields of 340–397- and >397-g tubers increased. With the decreasing plant population for the 5.4-stem seed, yields of <113- and 113–170-g tubers decreased, 170–284-g tubers remained constant, and 284–340-, 340–397- and >397-g tubers increased.

The age- and spacing-induced shifts in tuber size distribution are clearly evident when yields were expressed as percentage marketable yields (Fig. 1). Planting density had the greatest impact on tuber size distributions from the 2.8-stem seed lot. At 25-cm spacing, yields of tubers over 340 g accounted for 43 % of marketable yield (Fig. 1a). Size distributions shifted to favor even higher percentage (54 %) oversize (>340-g) tubers at 35-cm spacing but substantially lower percentage (22 %) at 15-cm spacing. The 170–284-g tubers dominated the other size classes at 15-cm spacing, accounting for 36 % of marketable yield. Crop values at 35-cm spacing were 8.2 (process) and 25 % (seed) lower than at 25-cm spacing, reflecting the negative effects of increased spacing on marketable yield and oversize tubers in frozen process and seed markets, respectively. In contrast, the significant shift toward higher percentage of <284-g tubers at 15-cm spacing contributed (along with the yield increase) to marginal increase (4 %) in frozen process value and substantial increase (39 %) in seed value (extra seed cost accounted for).

The marketable yield profiles produced by the 5.4-stem, age-primed seed were dominated by 170–284-g tubers (~35 %) at all spacings (Fig. 1b). Although attenuated, the changes in tuber size distribution from age-primed seed with planting density were similar to those described for the 2.8-stem seed lot. Relative to the conventional 25-cm spacing, tuber size distribution favored a greater percentage of tubers over 284 g at 35-cm spacing and less than 170 g at 15-cm spacing. Marketable yield of the high-stem seed matched that of the low-stem seed at 25- and 35-cm spacing; however, process values from the 5.4-stem seed at 15, 25, and 35-cm spacing were only 80, 87, and 87 %, respectively, of that produced by the 2.8-stem seed planted at conventional (25-cm) spacing. On the other hand, seed values produced by the age-primed seed were 162 % (15 cm), 152 % (25 cm), and 135 % (35 cm) of the 2.8-stem seed lot planted at 25 cm spacing and 116 % (15 cm), 109 % (25 cm), and 97 % (35 cm) of the 2.8-stem seed lot planted at 15 cm spacing. The tuber size distribution profiles produced by older seed of cv. Ranger Russet were

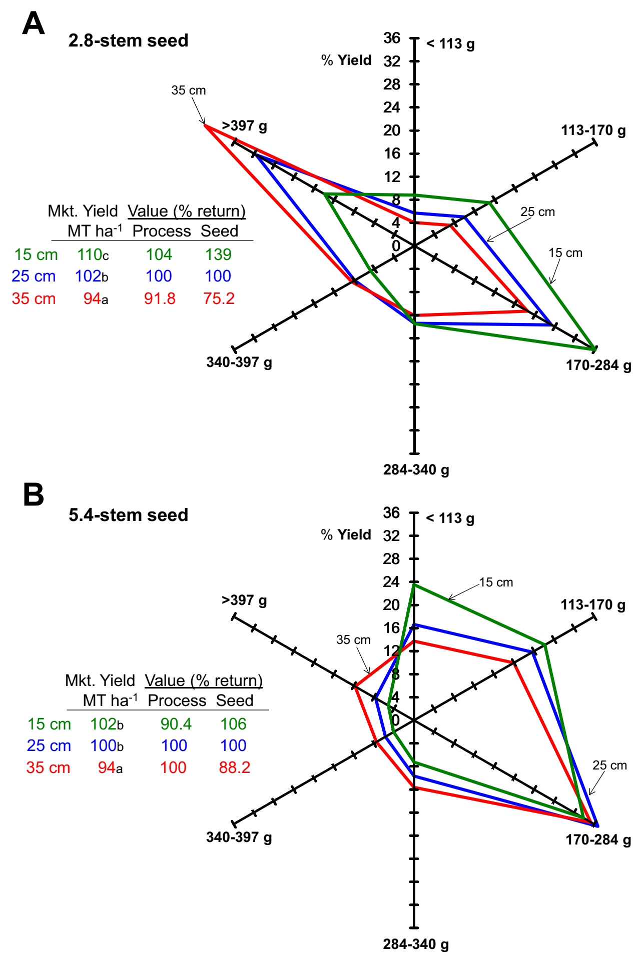

Fig. 1 Polygonal plots illustrating the shifts in tuber size distributions and crop values (*inset tables*) for low- (**a**) and high-stem (**b**) seed of cv. Ranger Russet planted at three in-row spacings. Seed tubers were age primed by storing at 12 and 32 °C for 80 and 720 DD (4 °C base) directly after harvest and then held at 4 °C (95 % RH) for the remainder of a 195-day storage period, resulting in the low- and high-stem seed, respectively. The yields of <113-, 113–170-, 170–284-, 284–340-, 340–397-, and >397-g U.S. No. 1 tubers are plotted as percent marketable (Mkt) yield on each of the six axes. *Inset tables* show crop values for direct-to-frozen process and seed markets (seed costs subtracted). Data are averaged over three growing seasons (2004–2006; Othello, WA) with two seed sources in years one and two and one seed source in year three (five seed-source years represented, $n = 25$). ANOVA for yield data is summarized in Table 2. *Letters* (Mkt yield) indicate mean separation (LSD, $P < 0.05$) across all six treatments

therefore more lucrative for seed production compared with younger seed at equivalent spacing, despite the higher marketable yield of younger seed at 15-cm spacing.

NAA Studies

Age priming for 80 and 600 DD produced seed that averaged 2.8 and 4.8 stems, respectively. On average, plants from the 4.8-stem seed emerged sooner than from the younger (2.8-stem) seed (Fig. 2a, b; Age × DAP, $P < 0.01$). Although NAA treatment delayed emergence ($P < 0.01$) from both seed lots, the response was greatest for the younger seed and equal for all three NAA concentrations. In contrast, the NAA-induced delay in emergence from the 4.8-stem seed was concentration dependent (Age × NAA × DAP, $P < 0.01$) and these effects were clearly evident at 31 DAP (Fig. 3a). By 38 DAP (Fig. 2), plant emergence had reached 95–100 % for the older seed compared with 75–100 % for the younger seed. Greater than 96 % emergence was achieved by 49 DAP and full emergence (100 %) from all treatments was achieved by stem count (55–62 DAP, depending on the year).

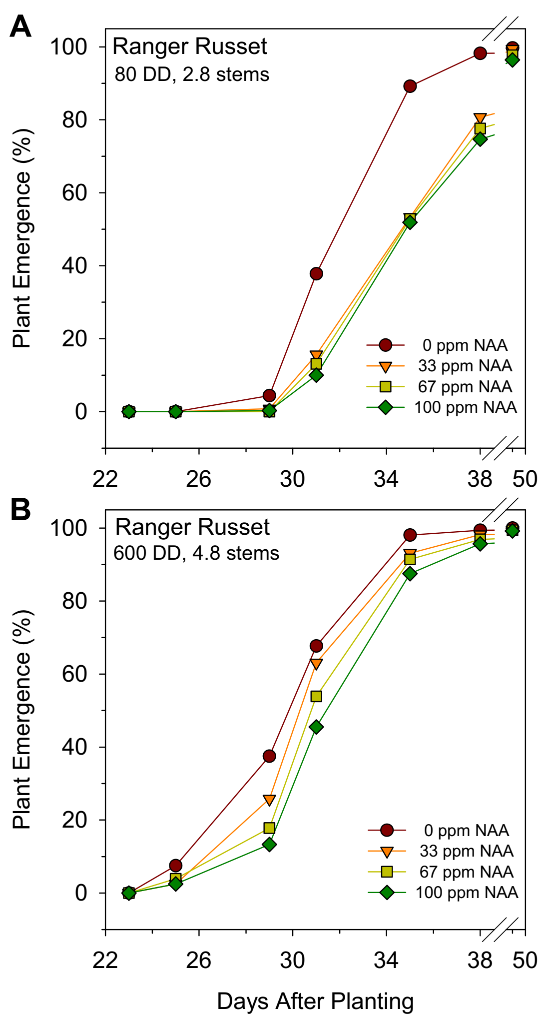

Fig. 2 Time course of plant emergence (%) from low- (**a**) and high-stem (**b**) seed of cv. Ranger Russet as affected by treatment of seed with 1-naphthaleneacetic acid (NAA). Seed tubers were age primed for 80 and 600 DD as described in Fig. 1. Data are averaged over three growing seasons ($n = 15$) (2007–2009; Othello, WA). Age ($P < 0.01$), NAA ($P < 0.01$), days after planting (DAP) ($P < 0.01$), Age × NAA × DAP ($P < 0.05$)

Treatment of seed with NAA decreased the number of stems per seed piece and this effect was greatest for the age-primed (600 DD) seed (Age × NAA, $P < 0.01$) (Fig. 3b). Stem numbers from the age-primed seed fell from 4.8 (non-treated) to 3.0 as NAA concentration increased to 100 mg L^{-1}, resulting in complete restoration of apical dominance to equal that expressed by younger seed. The non-treated 4.8-stem seed averaged 10 tubers per plant versus 8.4 tubers for the 2.8-stem seed (Fig. 3c). Tuber number per plant decreased linearly with increasing NAA concentration for both seed lots. Consistent with the restoration of apical dominance, the number of tubers per plant from the age-primed seed treated with 100 mg L^{-1} NAA was equal to that produced by the non-treated, 2.8-stem seed. The average tuber fresh weight of non-NAA-treated 80-DD seed was 20 % higher than age-primed seed and was not affected by NAA treatment (Fig. 3d). Tuber fresh weight increased (9 %) with increasing NAA applied to the 600-DD, age-primed seed.

Age priming had no effect on the total yields (Table 3). Yield from the 2.8-stem seed treated with 67 and 100 mg L^{-1} NAA was 9.8 % lower on average than non-NAA-treated seed. Although total yield from the 4.8-stem seed treated with 67 mg L^{-1} NAA was 9 % less than the non-treated control, the other NAA treatments produced equivalent yields and trends with NAA concentration were not well defined. U.S. No. 1 yield (excludes <113-g tubers) produced by non-NAA-treated 600-DD seed was 11 % lower than from 80-DD seed and, except for lower yield from the 67 mg L^{-1} 80-DD treatment, NAA had no effect. Age priming had no effect on marketable yields (U.S. No. 1 + <113-g tubers) where the effects of NAA were the same as for total yields. On average, the 600-DD seed produced substantially higher yields of less than 170-g tubers and lower yields of tubers greater than 284 g than 80-DD seed. The effect of NAA on yields of the various tuber size classes was the same regardless of seed age (that is, no age × NAA interactions were apparent). On average, yields of the two smallest tuber size grades decreased 18 % with increasing NAA concentration (MT $ha^{-1} = 12.5 - 0.023$ [NAA], $R^2 = 0.97$, $P < 0.01$), whereas yields of 284–340-, 340–397- and >397-g tubers remained relatively constant.

As percent marketable yield, tuber size distribution from the 80-DD, 2.8-stem seed favored 170–284-g (31 %) and oversize (>397 g) (24 %) tubers (Fig. 4). The marketable yield profile from 600-DD 4.8-stem seed was dominated (38 %) by 113–170- and <113-g tubers. With increasing NAA concentration on 600-DD seed, the percentage of <113-g and 113–170-g tubers fell, whereas tubers >284 g increased an equivalent amount (Table 3), culminating in a significant NAA-induced shift from smaller to larger tubers with 100 mg L^{-1} NAA (Fig. 4). In

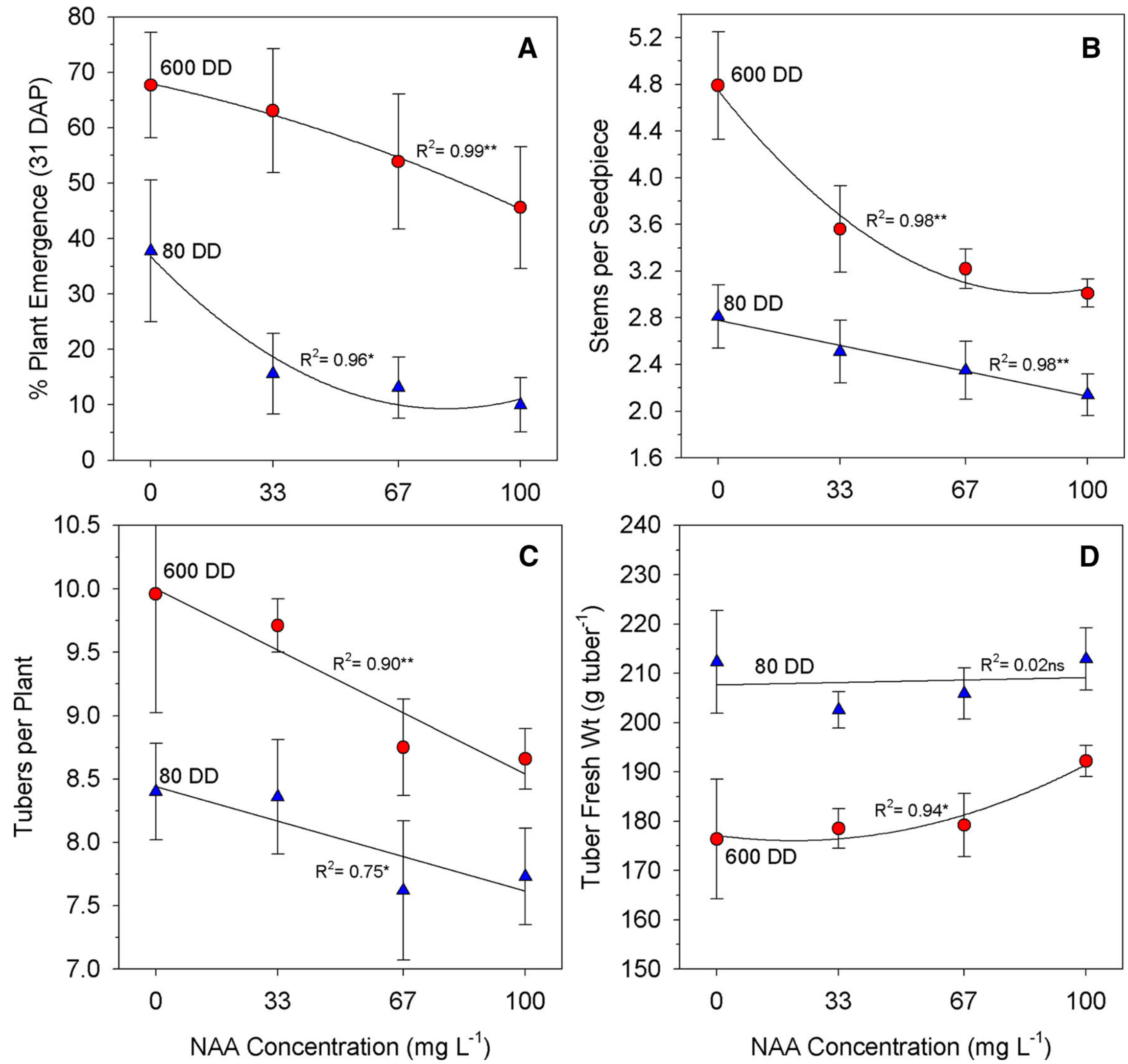

Fig. 3 Effects of age priming and 1-naphthaleneacetic acid (NAA) seed treatments on plant emergence (**a**), stem numbers (**b**), tubers per plant (**c**), and average tuber fresh weight (**d**) of cv. Ranger Russet. Seed tubers were age primed for 80, and 600 DD as described in Fig. 1. Data are averaged over three growing seasons ($n = 15$) (2007–2009; Othello, WA). *Bars* indicate ± SE. $^{*}P < 0.05$ and $^{**}P < 0.01$ for correlation coefficients; *ns* not significant. Regression equations: **a** 80 DD, $\% = 36.7 - 0.69[\text{NAA}] + 4.32e^{-3}[\text{NAA}]^2$; 600 DD, $\% = 67.9 - 0.14[\text{NAA}] - 8.37e^{-4}[\text{NAA}]^2$; **b** 80 DD, $\text{stems} = 2.78 - 6.49e^{-3}[\text{NAA}]$; 600 DD, $\text{stems} = 4.75 - 0.040[\text{NAA}] + 2.31e^{-4}[\text{NAA}]^2$; **c** 80 DD, $\text{tubers} = 8.44 - 8.26e^{-3}[\text{NAA}]$; 600 DD, $\text{tubers} = 10.0 - 0.015[\text{NAA}]$; **d** 600 DD, $\text{g tuber}^{-1} = 177 - 0.10[\text{NAA}] + 2.46e^{-3}[\text{NAA}]^2$

contrast, NAA had no appreciable effect on tuber size grades as percent marketable yield from the 80-DD seed, and therefore the size distribution from the non-treated 80-DD seed is compared with the non-treated and 100 mg L^{-1} NAA-treated 600-DD seed in Fig. 4. The marketable yields (Fig. 4 inset table) for these treatments were statistically equivalent, averaging 78.2 MT ha^{-1}. Hence, when calculated at equivalent yields to reflect the impact of treatments on tuber size distribution, process values from the non-treated and NAA-treated (100 mg L^{-1}) 600-DD seed were 92 and 97 % of non-treated 80-DD seed, respectively. Seed values from the 600-DD seed were 114 (non-treated) and 108 % (100 mg L^{-1} NAA) of the non-treated 2.8-stem seed (Fig. 4 inset table). Consistent with results from the spacing studies, the 600-DD high-stem seed produced a tuber size distribution profile that was more lucrative for seed than process market and the age-induced decline in value for frozen process was nearly recouped by treatment with NAA.

Table 3 Effects of auxin (NAA) seed treatments on tuber yields and size distributions produced by cv. Ranger Russet seed expressing high (2.8 stems) and low (5.4 stems) apical dominance

Seed age (degree-days)	NAA (ppm)	Tuber yield (MT ha^{-1})								
		Total	U.S. No. 1	<113 g	113–170 g	170–284 g	284–340 g	340–397 g	>397 g	Mkt Yld[a]
80 DD (2.8 stems)	0	81.8	72.6	8.06	11.9	25.3	8.86	7.44	19.1	80.7
	33	77.6	68.8	8.03	11.9	25.7	9.71	6.31	15.3	76.9
	67	72.2	63.4	7.64	10.5	22.0	8.15	7.06	15.8	71.1
	100	75.3	67.5	7.29	10.4	22.6	9.65	7.18	17.6	74.7
600 DD (4.8 stems)	0	79.0	64.8	13.2	16.5	23.7	6.57	5.36	12.8	78.1
	33	79.3	67.3	11.6	16.6	24.9	7.89	5.38	12.6	79.0
	67	71.5	60.7	10.4	14.8	23.2	7.87	4.87	10.1	71.1
	100	76.4	66.4	9.56	13.7	23.6	8.30	6.13	14.6	75.9
$LSD_{0.05}$		6.2	6.4	3.16	2.89	3.24	2.22	1.61	2.1	5.7
Age[b]		NS	0.05	0.01	0.01	NS	0.01	0.01	0.01	NS
NAA_{LT}		0.01[c]	NS	0.05	0.01	0.05	NS	NS	NS	0.01
NAA_{QT}		0.05	NS	NS	NS	NS	NS	NS	0.05	NS
NAA_{dev}		0.05	0.05	NS	NS	0.05	NS	NS	NS	0.05
Age × NAA_{LT}		NS	NS	NS	NS	NS	NS	NS	NS	NS
Age × NAA_{QT}		NS	NS	NS	NS	NS	NS	NS	NS	NS
Age × NAA_{dev}		NS	NS	NS	NS	NS	NS	NS	NS	NS

The 2.8- and 4.8-stem seed treatments were produced by storing seed at 12 and 32 °C for various periods immediately after harvest to accumulate 80- and 600-degree-days, respectively (4 °C base). The seed was then held at 4 °C for the remainder of storage (ca 195 days total). Seed was cut and treated by immersing in solutions of NAA containing 0.1 % Tween 20 approximately 4 days prior to planting. Data are averaged over three growing seasons

NS not significant

[a] Market (Mkt) yield includes U.S. No. 1 yield plus yield of <113-g tubers

[b] Sources of variation; LT, linear trend; QT, quadratic trend; dev, deviation from quadratic

[c] Significance levels for the various sources of variation ($P < 0.01$ or 0.05)

Discussion

The overall objective of these studies was to determine the extent to which in-row spacing and NAA treatments can alter stem numbers, tuber set, and size distribution of seed tubers expressing low and high apical dominance. Various factors during production, handling and storage of seed interact to affect the physiological age of seed at planting, which in turn affects the rate of plant emergence, stem numbers, tuber set and ultimate tuber size distribution at harvest (Iritani and Thornton 1984; Struik 2007a). The degree of apical dominance is indicative of the physiological age of a seed lot (Eshel and Teper-Bamnolker 2012), and tuber set and size distribution are directly related to stem number (Knowles and Knowles 2006). Adjusting in-row spacing to either increase or decrease tuber size, within the environmental constraints of a growing area, is an effective technique to maximize crop value in relation to market requirements for tuber size (Schotzko and others 1984; Bohl and others 2011). Therefore, if the relative age of a seed lot is known in terms of expected stem numbers prior to planting, it should be possible to adjust in-row spacing to alter final tuber size distribution for maximum crop value, since in-row spacing has no effect on apical dominance (Table 1; Bohl and others 2011). From a commercial production standpoint, the fundamental question is: Can a physiologically older, high-stem seed lot be planted at wider spacing to produce the average tuber number per hectare, yield and size profile of a younger, low-stem seed lot planted at conventional or closer in-row spacing? If achievable, then age primed, high-stem seed would be economically advantageous over younger, more apically dominant seed due to less seed required at the reduced planting density (for example, 29 % less seed required to plant at 35 cm versus 25 cm). Moreover, the potential decrease in number of tubers produced per hectare at wider spacing may not be an issue with age-primed seed because of the higher tuber set response associated with reduced apical dominance.

The consequence of the age-induced loss in apical dominance (Table 1) was an extreme disparity in stem density per hectare such that only a small overlap occurred

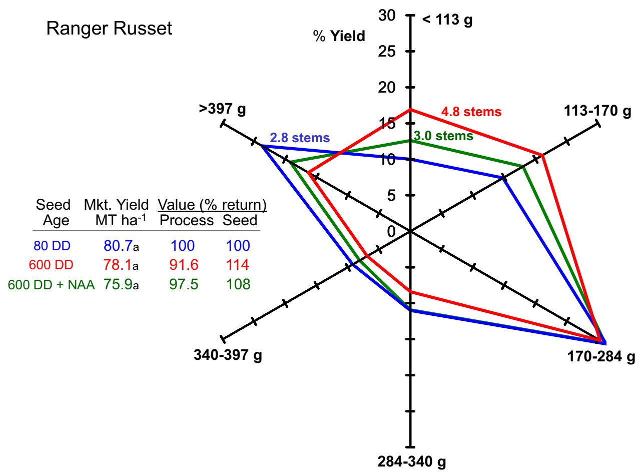

Fig. 4 Polygonal plots showing the effects of seed age (degree days, DD) and 1-naphthaleneacetic acid (NAA, 100 mg L^{-1}) on shifts in tuber size distributions, marketable (Mkt) yields and crop values (*inset tables*) for low- (2.8 stems, 80 DD) and high-stem (4.8 stems, 600 DD) seed of cv. Ranger Russet. Seed tubers were age primed as described in Fig. 1. Yields of the tuber size classes are plotted as percent marketable yield. Marketable yields (*inset table*) did not differ among these treatments. Crop values (*inset table*) for direct-to frozen process and seed markets have thus been normalized to the average yield (78.2 MT ha^{-1}). NAA had no appreciable effect on tuber size distribution of 80-DD seed as percent marketable yield. Data are averaged over three growing seasons ($n = 15$) (2007–2009; Othello, WA). Yield data are summarized in Table 3. *Letters* (Mkt yield) indicate mean separation (LSD, $P < 0.05$)

between the low- and high-stem treatments (from 179,000 to 205,000 stems ha^{-1}) over the range of planting densities. Using the linear relationships describing changes in total yield with stem density per ha for each age, the yields at a density of 198,000 stems ha^{-1} were compared. To produce that stem density, the 80-DD seed would require an in-row spacing of 15 cm and would yield 111.3 MT ha^{-1} [total yield $= 85.3 + 1.313e^{-4}$(stems ha^{-1}), $R^2 = 0.95$, $P < 0.05$]. In contrast, the 720 DD seed would need to be planted at 34 cm, resulting in a yield of only 97.6 MT ha^{-1} [total yield $= 89.9 + 3.746e^{-5}$(stems ha^{-1}), $R^2 = 0.88$, $P < 0.05$]. Clearly, physiological age-induced stem numbers ha^{-1} from the 720-DD seed lot do not entirely equate to spacing-induced stems ha^{-1} from the non-aged seed with regard to total yield. The study thus revealed a relatively small but significant effect of seed age on total yield that is not entirely attributable to differences in stem density for cv. Ranger Russet.

Total, U.S. No. 1 and marketable yields are only gross indicators of crop value. Contracts are largely based on tuber grade, size and quality characteristics (gravity, bruise-free, etc.) that differ for seed versus fresh market versus processing potatoes. Seed age and spacing affected the yields of six tuber size classes (Table 2) and, as percent marketable yield, spacing was a factor in five out of the six (Fig. 1). These results prompted an economic analysis of the marketable yields. The 2.8-stem seed achieved its highest commercial value at 15-cm spacing, whether the target market was seed or process (Fig. 1a). This high density planting shifted tuber size distribution relative to 25 and 35-cm spacings to favor the 113–284-g tubers while minimizing the percentage oversize (>397-g) tubers. The 5.4-stem seed demonstrated less plasticity in tuber size distribution response to in-row spacing compared with the 2.8-stem seed. This older seed was most favorably spaced at 15 cm for seed production, returning 16 and 61 % more value than the 2.8-stem seed planted at 15 or 25-cm spacing, respectively, despite the significantly higher marketable yield from younger seed at 15-cm spacing. For direct-to-process market, tuber size distribution of the 5.4-stem seed, however, was optimized for maximum value at 25- and 35-cm spacings, even though the marketable yield at 35 cm was significantly lower than at 15 or 25 cm (Fig. 1). The sparsest plant population (35 cm) produced the highest yields of the three largest tuber size categories while minimizing undersize tubers (<113 g) that have little value in processing. However, process value of tubers produced by the 5.4-stem seed at 35-cm spacing remained 13 % less than the 2.8-stem seed at conventional (25-cm) spacing. Therefore, adjusting in-row spacing to improve tuber set and grade in relation to market requirements only partly compensated for the higher stem numbers produced by age-primed seed.

Results of the seed age by in-row spacing trials are depicted in Fig. 5a where the number of tubers and relative average tuber sizes are in scale with the results presented in Tables 1 and 2. The schematic does not, however, illustrate the variation in tuber size distribution within a treatment, as depicted in Fig. 1. In-row spacing clearly affected tuber number and size development for both low- and high-stem seed (Fig. 5a). In general, tuber number and average mass per tuber increased with wider spacing, a well-established and widely reported response (Rykbost and Maxwell 1993; Tarkalson and others 2011). However, tuber number was affected by an interaction between seed age and spacing (Table 1; Fig. 5a). On average, plants from age-primed seed set seven more tubers as spacing increased from 15 to 35 cm, versus only three extra tubers for plants from younger seed, which greatly limited the increase in average tuber fresh weight (Table 1), shift in tuber size distribution toward larger tubers, and increase in crop value (frozen process contract) from the high-stem seed (Fig. 1). Although the effect of seed age on tuberization and increased tuber set is well documented (Knowles and others 1985; Struik 2007b), the greater responses of plants from age-primed seed to decreasing plant population has hitherto not been reported, and partly explains why the tuber size distribution profile and crop values from the 5.4-

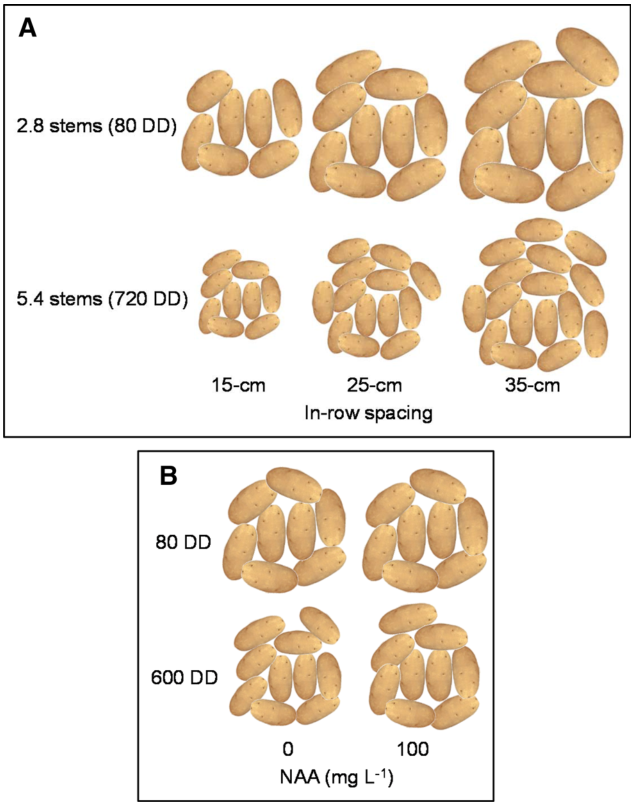

Fig. 5 Schematic illustration of the relative effects of in-row seed spacing (**a**) and 1-naphthaleneacetic acid (NAA) seed treatment (**b**) on tuber number per plant and average tuber size produced by seed expressing high (2.8 stems) and low (4.8 and 5.4 stems) apical dominance. Low apical dominance was produced by age-priming seed for 600 DD (4.8 stems) and 720 DD (5.4 stems) at high temperature during storage. While NAA treatment restored apical dominance (Fig. 3**b**), the non-treated tubers averaged 2.8 (80 DD) and 4.8 stems (600 DD) per seed piece. In both **a** and **b**, the relative tuber number and average size are scaled to accurately portray treatment effects. The variation in tuber size distribution is not accurately represented

stem seed at 35-cm spacing remained significantly different than the younger seed planted at conventional and closer spacing.

Altering the expression of apical dominance with plant growth regulators offers an alternative approach to in-row spacing for maximizing crop value in relation to market requirements for tuber size. Apical dominance is modulated by interplay between auxin, cytokinin, strigolactones, (Young and others 2014 and references therein) and sucrose supply (Mason and others 2014). The mechanism is complex, likely differs between plant species and organs (for example, above ground versus below ground stems), and remains to be fully elucidated. However, from a practical standpoint, the expression of apical dominance can be effectively altered in potato seed tubers with gibberellin and auxin. Treatment of seed with gibberellins prior to planting reduces apical dominance, resulting in increased stem numbers, tuber set and shift in tuber size distribution toward increased yields of smaller size tubers, with associated increase or decrease in crop value depending on market requirements for tuber size (Blauer and others 2013a). Conversely, preplant treatment of seed with auxin reduces stem numbers (Knowles and others 1985; Mikitzel and Knowles 1990; Kumar and Knowles 1993); however, the extent to which auxin can be used to completely restore apical dominance, tuber set, size distribution, and crop value to an age-primed seed lot is unknown.

The restoration of apical dominance in age-primed seed with NAA was dose-dependent. Treating 600-DD seed with 100 mg L^{-1} NAA restored apical dominance and decreased tuber number per plant to equal that of the 80-DD seed (Fig. 3). Nevertheless, the average tuber weight produced by NAA-treated 600-DD seed remained 9 % (20 g $tuber^{-1}$, $P < 0.05$) lower than that produced by the non-treated 80-DD seed (Figs. 3, 5b), indicating that the exogenous auxin treatment did not fully restore all aspects of young seed productivity. These results provide further evidence that tuber age has a small but significant residual effect on productivity beyond that attributable to loss of apical dominance.

As percentage marketable yield, tuber size distribution from the 80-DD seed was relatively insensitive to NAA when compared with that produced by the 600-DD seed. In accordance with the restoration of apical dominance, the high rate of NAA (100 mg L^{-1}) shifted the tuber size distribution produced by 600-DD seed from relatively high percentage of <170-g tubers to higher percentage of >284-g tubers, whereas the percentage of 170–284-g tubers remained constant relative to the non-treated seed (Fig. 4). The process market rewards premiums for crops having at least 56 % of tubers >170 g, whereas the undersized (<113 g) tubers are of minimal value (Pavek and Knowles 2009). It is significant to note that NAA reduced this undersized category by nearly 28 % in the crop produced by 600-DD seed. The shift in tuber size distribution increased the process value of 600-DD seed by \$500 ha^{-1}, which was only 2.9 % less than that produced by the non-treated 80-DD seed. NAA thus appears well suited to partly restore the value of process market crops produced by older seed, or to add value to seed of cultivars that inherently produce too many stems, through its effects on apical dominance, tuber set and tuber size distribution.

In summary, tuber set, size distribution, and crop value produced by seed lots expressing varying degrees of apical dominance can be effectively manipulated by varying planting density (in-row spacing) or treating the seed prior to planting with NAA. The recommended planting densities and effective concentrations of NAA to maximize value will depend on cultivar, the degree of expression of apical dominance in the seed at planting, and the specific market requirements for tuber size. A major challenge to fully exploiting these management techniques to effectively manipulate tuber size distribution for enhanced value is estimating the physiological age of seed in terms of stem numbers prior to planting. Future research in this area should focus on developing reliable biochemical and/or molecular markers that can accurately predict and resolve differences in the degree of apical dominance among commercial seed lots.

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