Improving Seedling Vigor in Sexual Seeds of Potato Under High Temperature

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Abstract. Sexual seeds of potato (*Solanum tuberosum* L.) usually emerge poorly under high-temperature conditions (> 25 C). A seedling vigor study was conducted during the warm season (1988-89) in Lima, Peru, and the results of two representative tests are reported. Two presowing treatments and a rinsed control were compared for seedling-stand establishment in a screenhouse with old (>18 months) and new (> 6 months) sexual seeds of three potato crosses. The treatments consisted of soaking the seed in solutions of $\text{KNO}_3 + \text{K}_2\text{P}_2\text{O}_7$ at -1.0 MPa (priming) and gibberellic acid at 1500 ppm (GA1500). Seedling vigor was lower at 34C (February test) than at 29C (November test). In both tests, overall seedling performance was highest in seed of the cross Atlantic $\times$ LT-7. Old seed was more vigorous than new seed, particularly when the crosses Atzimba $\times$ R128.6 (B2) and Serrana $\times$ LT-7 (C1) were tested at 34C. Priming increased percentage of early (10 days) emergence over the other treatments at 34C and increased seedling dry weight in both tests. GA1500 increased percentage of final (17 days) emergence in crosses B2 and C1, as compared to rinsing, except at 29C, where there were no significant differences in old seed. For sowing true potato seed at high temperature, a) the genotype is a crucial factor, b) sufficient seed storage (> 18 months) may be essential, and c) seed priming is more effective than the standard GA1500 treatment.

High-quality or virus-free seed tubers for potato production in tropical environments are generally unavailable or must be imported. Sexual seed of potato or true potato seed (TPS) is mostly virus-free and offers a practical alternative to seed tubers (Malagamba, 1988). However, TPS is dormant at harvest, and germination is often erratic even after prolonged storage (Simmonds, 1963, 1968). Young TPS seedlings also generally grow with low vigor and, therefore, the seed is usually sown under favorable conditions in nurseries to produce seedling tubers (Wiersema, 1986). These small potatoes are stored as high-quality seed tubers until the subsequent season for planting the vegetatively propagated crop.

The principal causes for the poor early performance of TPS are: 1) the progenies have not been selected for seedling emergence and development characteristics (Pallais, 1987), 2) the production and storage of high-quality (vigorous during emergence) seed has only recently been addressed (Pallais et al., 1985, 1987, 1989, 1990; Pallais and Fong, 1989), and 3) the seed is usually sown without taking into consideration that the in-

hibiting effects of dormancy may last for many years after harvesting the TPS (Simmonds, 1968). Gibberellic acid (GA) at 1000 to 2000 ppm traditionally has been used to overcome TPS dormancy (Spicer, 1961). However, a germinated embryo is not sufficient evidence of dormancy release because seeds can also express dormancy during seedling development. Examples of reduced root and hypocotyl growth, as well as clear differences in the behavior of the cotyledons developing from dormant embryos, have been described in many species (Côme and Thévenot, 1982). Recently, evidence has been provided that while GA does promote germination in newly harvested TPS, subsequent seedling growth is diminished by this treatment (Pallais, 1989).

Most TPS genotypes investigated require a period of at least 6 months of seed after-ripening following harvest to ensure that most of the seeds will emerge from the soil and grow at an acceptable rate (Pallais et al., 1990).

The problems of seedling emergence in TPS are greatly increased under warm conditions (Clark and Stevenson, 1943; Ghate et al., 1983; Malagamba, 1988). Optimum temperatures for TPS germination range from 15 to 20C (Gallagher and Navbi, 1985; Lam, 1968), and emergence from soil can be severely inhibited at >25C. Shading of the seedbed to lower soil temperature during germination and early seedling growth is a requirement for producing seedling tubers in many tropical environments (Malagamba, 1983; Wiersema, 1986). Studies on practical and effective methods to increase seedling emergence under high-temperature conditions are needed because TPS technology has the potential for adoption in tropical regions. Seed presowing techniques, such as osmotic priming, have demonstrated potential to increase seedling emergence under unfavorable temperatures in many species (Bradford, 1986). Priming of TPS in a solution of $\text{KNO}_3 + \text{K}_2\text{P}_2\text{O}_7$ at -1.0 MPa after 6 months of seed storage has been shown to be an effective seed treatment for enhancing seedling emergence (Pallais, 1989; Pallais et al., 1990).

The objectives of this study were to: a) evaluate the effects of priming and GA presowing treatments on early seedling performance of TPS sown under high-temperature conditions, b) determine if any residual dormancy effects remain in the seed after a storage period of 7 to 22 months, and c) observe differences in genotype response.

Various experiments were run during Nov. to Mar. 1988-89 in Lima, Peru, and the results of two representative tests are reported here. High-quality TPS produced in a large plot in Osorno, Chile, in Apr. 1987 (old seed) and 1988 (new seed) were sampled at random for this study from bulk lots after seed drying. The TPS crosses tested were: Atlantic $\times$ LT-7 (A1), Atzimba $\times$ R128.6 (B2), and Serrana $\times$ LT-7 (C1). These TPS progenies were selected

Fig. 1. Mean seedling dry weight as affected by seed age in three TPS crosses.
²For comparisons among all means.

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Table 1. Analysis of variance for the criteria of potato seedling vigor in the November and February tests.

Source	df		Sums of square percentage and their significance ^{z,y}						Reps	
	November	February	Emergence (%)		Dry wt/plant		November	February	November	February
			November	February	November	February				
TPS cross (TC)	2	2	25.5**	14.8**	19.8**	15.6**	17.8**	10.4**	30	96
Error (a)	6	8	0.3	0.6	0.4	1.6	1.1	3.6		
Seed age (SA)	1	1	33.9**	46.5**	21.1**	40.5**	41.0**	18.9**	144	45
TC × SA	2	2	13.0**	0.02 ^{NS}	10.3**	1.9**	2.4**	0.1 ^{NS}	48	15
Error (b)	9	12	2.0	1.7	1.5	3.0	0.9	1.6		
Presowing (PS)	2	2	2.0**	22.6**	5.0**	19.4**	21.9**	50.7**	96	30
PS × TC	4	4	1.8**	5.4**	3.4**	4.9**	2.1*	3.3**	32	10
PS × SA	2	2	3.2**	3.6**	7.4**	2.1**	0.3 ^{NS}	1.4*	48	15
PS × TC × SA	4	4	1.4**	0.5 ^{NS}	2.5**	2.4*	1.0 ^{NS}	2.3*	16	5
Error (c)	36	48	2.8	3.9	5.1	8.2	4.9	7.5		
Sampling error ^y	216		7.9		19.0		6.3			

^zRounded to nearest decimal.^yFour sub-samples for each of the four replications were evaluated.^{NS}, **, *Nonsignificant or significant at $P < 0.01$ or 0.05 , respectively.

Fig. 2. Mean seedling dry weight as affected by presowing treatments in three TPS crosses.

^zFor comparisons among all means.

at the International Potato Center (CIP) for their superior stability for producing high tuber yields under short-day conditions. After harvesting the mature berries at ≈ 11 weeks post-pollination, seeds were extracted and surface-sterilized by soaking them for 10 min in a 0.5% solution of sodium hypochlorite and then washing and drying them at 15C (35% RH) to $\approx 7\%$ moisture content (dry-weight basis). The seed was then transported to Lima for storage at room temperature ($\approx 22\text{C}$) until the time of treatments and evaluations.

The following treatments were applied to the seed before sowing: 1) osmoconditioning in KNO_3 at $118 \text{ mol}\cdot\text{m}^{-3}$ + K_2PO_4 at $90 \text{ mol}\cdot\text{m}^{-3}$ for 5 days (priming), 2) soaking in 1500 ppm of GA for 1 day (GA1500), and 3) maintaining untreated seed dry for 5 days in the presowing environment for use as a control (rinsing). The seeds were evenly distributed over a single layer of Whatman #1 filter paper, which was either dry (rinsing) or soaked in 5 ml of the presowing solutions, and placed inside 9-cm covered petri dishes sealed with Parafilm M. All treatments were conducted inside a seed germinator at $15 \pm$

1C under alternating 12-h light and dark periods. On the 4th day of priming, the GA1500 treatment was started. On the 5th day, all lots were rinsed under running tap water for 2 min, then dried to $\approx 8\%$ moisture content, and stored for 3 days at room temperature before sowing.

Screenhouse tests were performed on early seedling vigor at the CIP-Lima Experiment Station in Nov. 1988 and Feb. 1989. Temperature in the testing environment was monitored with a hydrothermograph. Daily air means during the first 10 days after sowing were 29C day/15C night (November) and 34C day/19C night (February). The seed was sown on sterilized 1 sand : 1 peat medium in plastic flats. Twenty seeds were evenly sown in rows 10 mm deep and 25 cm long. In the November test, four replications per treatment were used; each block consisted of four rows that were evaluated individually. In the February test, five one-row replications were used. The experimental design consisted of a factorial split-split-plot, with TPS cross as the main plot, seed age as subplot, and presowing treatments as sub-subplot. The evaluations consisted of the percentage of emergence at 10 (early) and 17 (final) days after sowing and dry weight of seedling tops after cutting at soil level and drying for 48 h at 80C. Data were analyzed using standard statistical methods, the percentages of emergence were analyzed after arcsin transformation of the data, and LSD values were determined for comparisons between means according to the usual linear procedures (Steel and Torrie, 1980).

The analysis of variance is presented as the sums of square percentage in Table 1. Most interaction effects among the experimental factors were significant. In most cases, seed age was the most important single factor affecting the percentage of early and final emergence (Table 1). The main genotype effect, or TPS cross, was always important for all the criteria tested. The analysis also indicates that the presowing treatment was the least important variable on emergence in the November test. However, the importance of the presowing treatment increased substantially when seedling dry weight was evaluated in the November test. In the February

test, the presowing treatment had an important effect on all criteria evaluated, especially seedling dry weight.

November test. In cross A1, there were no significant ($P < 0.05$) effects of seed age or presowing treatments on the percentages of early and final emergence (Table 2). The percentage of early emergence in all seed lots of cross A1 was $\geq 95\%$ and final emergence was $\geq 97\%$. In seed of crosses B2 and C1, the percentages of early and final emergence were from 10% to 60% higher ($P < 0.05$) in old (19-month) seed than in new (7-month) seed, depending on the presowing treatment (Table 2). For all presowing treatments, both early and final emergence in old seed of cross B2 was 99%. In new seed of B2, early and final emergence were $\approx 20\%$ higher for the GA1500 or priming treatments than for rinsing. In old seed of C1, the percentages of early and final emergence were slightly ($\leq 8\%$) lower for the priming treatment than for the GA1500 ($\geq 96\%$) or rinsing ($\geq 93\%$) treatment. The difference in the percentage of early emergence between priming and rinsing was not significant. In new seed of C1, final emergence was 90% when GA1500-treated, 81% when primed, and 56% when rinsed. Old seed of all crosses produced seedlings with a higher dry weight than new seed, and within seed age lots, cross A1 seedlings had more dry matter than B2 and C1 (Fig. 1). Primed seeds had the highest seedling dry weights, and only in cross C1 did GA1500 increase dry weight above that of the rinsed control (Fig. 2).

February test. For all presowing treatments, the percentage of early emergence in old (22-month) seed of cross A1 was 75%, 2.5 times higher than in new (10-month) seed (Table 3). Early emergence in old seed of B2 was 60%, 3.3 times higher than in new seed; in old seed of C1 it was 44%, 11 times higher than in new seed. Irrespective of seed age, the priming treatment increased the percentage of early emergence, as compared to GA1500 or rinsing, except in seed of cross C1, where the difference in emergence between priming and GA1500 was not significant (Table 3). For all crosses, early emergence in old seed was higher when treated with GA1500 than when rinsed, and

Table 2. Effects of presowing treatment and seed age on the percentage of early (10 days) and final (17 days) emergence of three TPS crosses tested in November.^z

Presowing treatment	TPS cross											
	A1				B2				C1			
	10 days		17 days		10 days		17 days		10 days		17 days	
	Seed age											
	New	Old	New	Old	New	Old	New	Old	New	Old	New	Old
Priming	98 a	96 a	99 a	97 a	79 a	99 a	89 a	99 a	66 a	88 b	81 b	90 b
GA1500	95 a	98 a	99 a	99 a	77 a	99 a	90 a	99 a	60 a	96 a	90 a	97 a
Rinsing	96 a	98 a	98 a	99 a	57 b	99 a	68 b	99 a	31 b	93 ab	56 c	97 a

^zFor each cross and criterion, means are separated at $P < 0.05$ by boldface between columns and by different letters within columns.

Fig. 3. Effect of presowing treatments and seed age on seedling dry weight.

^zPRI = priming; GA = GA1500; RIN = rinsing.

^yFor comparisons among all means.

in new seed, the difference was not significant (Table 4). Within presowing treatments, the percentage of final emergence of all crosses was higher in old seed than in new seed, particularly for crosses B2 and C1 (Table 5). Within each seed age lot, the priming treatment increased final emergence, as compared with that of the GA1500 and the rinsing treatments, except in old seed of cross C1, where emergence for the GA1500 treatment was 96% and priming 75% (Table 5). The results on seedling dry weight were similar to those obtained in the November test (Figs. 1 and 2), except the GA1500 treatment did not increase dry weight in seed of cross C1 (Fig. 3). Primed seeds of cross A1 and priming old seed of crosses B2 and C1 produced the highest seedling dry weights (Fig. 3). The differences in dry weight between priming old seed of crosses B2 and C1 and the other treatments generally were greater in the February test than in the November test. The results also indicate that seedling dry weight in primed new seed of A1 was not significantly different from primed old seed of B2 or C1.

Considerable physiological enhancement of TPS vigor was shown to be possible by sufficient storage and the use of an effective presowing treatment, such as priming. As in previous reports (Pallais, 1989; Pallais et al., 1990), the standard GA1500 treatment used for TPS was shown to be practically ineffective for increasing seedling growth (Figs. 2 and 3), in spite of its generally promotive

effect on final emergence (Tables 2 and 5). A higher percentage of old (22-month) seed consistently emerged sooner at high temperature (February test) and produced seedlings with higher dry weight than new (10-month) seed (Tables 3 and 5, Fig. 3). The pivotal importance of the genotype when the seeds are sown closer to harvest was also demonstrated. In support of a previous report (Pallais et al., 1989), newly harvested seeds of cross A1 were generally more vigorous during emergence than those of the other crosses. Seed age was more important for crosses B2 and C1 than for A1. Priming was the most effective treatment for increasing seedling vigor, especially for crosses B2 and C1 when tested at high temperature (February test). The superiority of new seed of A1 for the production of seedling dry matter was also more evident at a high than at a favorable temperature (November test) (Fig. 3). Thus, the consideration of the temperature environment during testing may be critical for classifying different TPS progenies according to their ability to emerge and develop as seedlings in warm climates.

Varying levels of dormancy effects on the various criteria evaluated were observed among the three TPS crosses investigated, ranging from low dormancy in seed of cross A1 to high dormancy in C1. The TPS were tested after various seed storage periods at 22°C; lower temperatures would have increased the intensity of seed dormancy (Simmonds, 1968). At high temperature, the

GA1500 treatment considerably increased the percentage of final emergence in new seed of crosses B2 and C1, as compared with rinsing (Table 5). Only for old (22-month) seed of cross C1 was GA1500 more effective on final emergence than both the priming and the rinsing treatments. These results suggest that the seed of cross C1 was still partially dormant after 22 months of storage. Nevertheless, the residual dormancy in old seed of C1 was apparently concentrated in a small portion of the TPS genotypes in the population. Although final emergence in old seed of C1 was 75% for the priming treatment (Table 5), seedling dry weight in this treatment was not far below that of the best lot of A1 (Fig. 3). Individual seeds within a progeny apparently lose dormancy in storage at different rates. Some seeds of a given lot may be dormant, while most of the other seeds will either age in storage or lose their seed vigor potential. Therefore, increasing seeding rates, according to the proportion of dormant seeds, could be a solution for sowing partially dormant TPS at supra-optimal temperature. If a lower dormancy in individual seeds within a TPS progeny were found to be linked to desirable characteristics in the tubers produced from such seed, the solution proposed above could also result in an improvement of tuber uniformity at harvest.

Previous studies on TPS dormancy and germination consisted mainly of testing for final seed germination under favorable conditions in seed of unknown maturity or harvested up to 6 weeks postpollination (Clark and Stevenson, 1943; Gallagher and Navbi, 1985; Lam, 1968; Simmonds, 1963, 1968; Spicer, 1961). However, conclusions obtained with immature TPS are not likely to apply to mature seed harvested at 11 weeks (Kermode et al., 1986; Pallais et al., 1989), such as the seed for this study. An increased understanding is needed about the relationships between TPS dormancy and seedling vigor when high-quality (e. g., proper seed maturity) seed is sown at high temperature. This knowledge could be of benefit to breeders during selection for superior TPS progenies. Possible alternatives for ameliorating the effects of dormancy on seedling establishment of currently selected TPS progenies may also be found. The fact that seedlings from old seed were more vigorous than those from new seed, especially at high temperature, suggests that, as in other plant species, the nature of the after-ripening requirement in TPS is related to the progressive loss during storage of thermo-inhibiting factors present in the seed at harvest (Khan and Saminy, 1982). It seems that the decrease in TPS dormancy during storage provides the seed with an increasing ability to emerge and grow rapidly under high temperatures. It has been pointed out that the release of seed dormancy in weeds involves widening the range of environmental conditions suitable for germination (Karssen, 1982). Until seed dormancy has been sufficiently removed from TPS progenies by selection, TPS germination characteristics will resemble those found in natural populations of annual plants.

Table 3. Effects of seed age and presowing treatment on the percentage of early emergence of three TPS crosses tested in February.

Variable	TPS cross ²		
	A1	B2	C1
Seed age			
New	30 b	18 b	4 b
Old	75 a	60 a	44 a
Presowing			
Priming	74 a	69 a	35 a
GA1500	39 b	25 b	30 a
Rinsing	45 b	25 b	7 b

²Mean separation within columns for a given set of variables at $P = 0.05$.

Table 4. Effects of seed age and presowing treatment on the percentage of early emergence in three TPS crosses tested in February.

Presowing treatment	Seed age ²	
	New	Old
Priming	39 a	79 a
GA1500	3 b	59 b
Rinsing	10 b	41 c

²Mean separation within columns for a given set of variables at $P = 0.05$.

The seedling vigor improvements obtained in crosses B2 and C1 by priming old seed were the most dramatic result of this study (Tables 3 and 4, Fig. 3). In the future, priming of TPS is likely to be adopted by seed producers as an effective technique to improve seedling emergence. Studies on the storability of the priming effect are still needed. For example, the resistance of tomato seeds to deterioration in storage is decreased by priming (Argerich et al., 1989). Storing TPS for such long periods (22 months) is, however, impractical and a highly unlikely technique to be adopted by farmers in the tropics whose most pressing problem is the unavailability of clean potato seed. Moreover, when primed, 10-month-old seed of cross A1 was almost as vigorous as 22-month-old seed of B2 and C1. Therefore, it is possible that the most significant improvements of seedling vigor in TPS will result from selection for less dormant and more vigorous progenies.

From the results presented here, it can be concluded that the need for and current use of TPS in warm climates before proper after-ripening explain why the seed has proven to be unusable for producing potatoes directly (Vander Zaag et al., 1989) and why TPS is preferred for producing small seedling tubers under favorable conditions for planting the next season's vegetatively propagated crop. Seed priming and prolonged storage substantially increased seedling vigor in the three

Table 5. Effects of presowing treatments and seed age on final percentage of emergence of three TPS crosses tested in February.²

Presowing treatment	TPS cross					
	A1		B2		C1	
	Seed age					
	New	Old	New	Old	New	Old
Priming	83 a	95 a	66 a	98 a	45 a	75 b
GA1500	58 b	97 a	48 b	85 a	38 a	96 a
Rinsing	68 ab	79 b	18 c	70 b	7 b	52 c

²For each cross, means are separated at $P < 0.05$ by boldface between columns and by different letters within columns.

TPS progenies. However, the study clearly shows the essential importance of the genotype when more recently harvested seed (1 vs. 2 years) is sown under high temperatures. Genetic variability for seedling vigor traits crucial to sexually propagated crops is to be expected in the potato and must be sought if the potential of the TPS alternative to seed tubers for increasing potato production in tropical areas is ever going to be evaluated seriously.

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