Germination of Osmotically Primed Asparagus and Tomato Seeds after Storage up to Three Months

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Abstract. **The influence of two drying regimes and two storage temperatures of primed asparagus (*Asparagus officinalis* L.) and tomato (*Lycopersicon esculentum* Mill.) seeds on germination after storage up to 3 months was examined. Seeds of 'Mary Washington' asparagus and 'Ace 55' tomato primed in synthetic seawater (–1.0 MPa, 20C, 1 week, dark) were surface-dried at 20C and 50% relative humidity (RH) for 2 h (42% to 49% moisture) or dried-back at 20C and 32.5% RH for 48 h (moisture = 13% tomato and 22% asparagus). These and nonprimed seeds were stored in tight-lidded metal cans and heat-sealed plastic pouches at 4 or 20C for up to 3 months before germination at 20C. After 3-month storage, primed surface-dried asparagus seeds stored at 4C had greater germination percentage and rate than nonprimed seeds, surface-dried seeds stored at 20C, or primed dried-back seeds. Dried-back primed tomato seeds had higher germination percentage than surface-dried primed seeds after 2 or 3 months of storage, with storage temperature having no effect on germination perecentage or rate. In a further study, primed surface-dried and primed dried-back seeds stored at 4 or 20C for 1.5 months in sealed containers were germinated at 15, 25, or 35C under low (–0.05 MPa) or high osmotic stress (–0.4 MPa). Primed surface-dried asparagus seeds stored at 4C, compared to nonprimed seeds, surface-dried seed stored at 20C, or primed dried-back seeds, had greater germination percentage at 15 and 35C and low osmotic stress, and higher germination rate at 15 or 25C. Primed tomato seeds had greater germination percentage than nonprimed seeds only at 35C and low osmotic stress, and higher germination rate at 15 or 25C. Storage of primed tomato seeds at 4C rather than 20C increased germination rate at 15 or 25C, and increased germination percentage at 35C and low osmotic stress. For maximal seed viability and germination rate after 1.5 to 3 months of storage, primed asparagus and tomato seeds should be stored at 4C rather than 20C; however, asparagus seeds should be surface-dried, and tomato seeds should be dried-back.**

Seed priming is a pre-sowing, controlled-hydration treatment in which quiescent seeds are exposed to an external water potential sufficiently low to prevent radicle protrusion and yet stimulate physiological and biochemical activities (Bradford, 1986; Khan 1992). Primed seeds can have improved germination rate and uniformity, particularly under adverse seed-bed conditions such as low temperature (Pill and Finch-Savage, 1988), matric stress (Akers et al., 1987; Frett and Pill, 1989), salinity (Pill et al., 1991; Wiebe and Muhyaddin, 1987), and heat (Wurr and Fellows, 1984).

Seed-handling treatments following priming, however, can affect subsequent germination. Seed germination of tomato (Pill et al., 1991) and asparagus (Evans and Pill, 1989; Pill et al., 1991) is delayed in proportion to the extent of seed drying after priming. Seeds that are transferred directly from the priming solution to the germination medium have been considered "pregerminated" (Bradford, 1986) and can be suspended in a protective hydrophilic carrier gel, which then is delivered to the seed bed using fluid drilling (Pill, 1991).

Handling of primed seeds in the dry state has practical advantages for seedsmen and growers, but reports on the effects of extended storage of dried primed seeds on seed germination have been conflicting and limited to a few species. Primed and nonprimed tomato seeds retained high viability after 18-month storage at 10 or 20C and 6% moisture (Alvarado and Bradford, 1988). Primed seeds stored at 30C, however, particularly those primed in KNO_3 rather than polyethylene glycol, lost vigor and viability more rapidly than nonprimed seeds. Argerich et al. (1989) reported that both viability andgermination were unaffected by 4 or 30C storage for one year in nonprimed tomato seeds, or by 4C storage in primed seeds. At 30C, however, viability and germination rate of primed seeds were reduced markedly after 6 months of storage. These authors concluded that primed tomato seeds must be considered vigorous with a reduced storage life. While priming has speeded asparagus germination when seeds were dried for 2 days or less (Evans and Pill, 1989; Frett et al., 1991; Pill et al., 1991), the effects of longer storage of primed asparagus seeds on germination have not been reported. We know of no reports on the effects of seed moisture content during storage of primed seeds on subsequent seed viability and germination rate. Growers who prime their own seeds several months before planting need to know the extent of seed drying and the seed storage temperature that will retain the maxiumum benefits of priming.

We report here on two studies concerning primed tomato and asparagus seeds. The objective of the first was to determine germination percentage and rate of primed seeds that were surface-dried or dried-back and then stored at 4 or 20C for 1, 2, or 3 months. The objective of the second study was to determine the effects of seed-drying regime and subsequent storage temperature of primed seeds on germination at several temperatures and osmotically restricted water availability.

Materials and Methods

Seed storage duration. Seeds of 'Mary Washington' asparagus and 'Ace 55' tomato were primed in –1.0 MPa (20C, 1 week, dark)

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synthetic seawater (Instant Ocean, Aquarium Systems, Mentor, Ohio), priming conditions shown to be effective (Frett et al., 1991; Pill et al., 1991). Fifty seeds were randomly distributed on two layers of germination paper (Seed Germination Blotters, no 385; Seedboro Co., Chicago, Ill.) wetted with 20 ml priming solution in a 125 × 80 × 20-mm polystyrene box (Stewart Plastics, Croydon, U.K.). After priming, seeds were rinsed in deionized water.

Primed seeds were considered surface-dried when they could be singulated easily. Seeds were dried-back by equilibrating them for 48 h in the dark at 20C and 32.5% relative humidity (RH) (Frett and Pill, 1989). Primed (surface-dried and dried-back) and nonprimed seeds were placed in 40 mm diameter × 14 mm-tall seamless metal cans with tightly fitted lids (Ellisco Inc., Pennsauken, N.J.). Five cans (replications) were heat-sealed in 946-ml polyethylene pouches (Kapak, Fisher Scientific, Malvern, Pa.). The sealed pouches were stored in the dark for 1, 2, or 3 months at 4C (a standard refrigeration temperature) or 20C (a standard room temperature). Seed moisture, as percentage of wet weight, was determined by oven-drying ten, 100-seed replicates of each seed treatment for 1 h at 130C just before seed storage and at the end of each storage period.

Stored and nonstored seeds were germinated in 125 × 80 × 20-mm boxes containing two layers of germination paper wetted with 20 ml 0.5-fold Hoagland solution, version 1 (Hoagland and Arnon, 1938). The numbers of seeds germinated (radicles visible) at 20C in dark were recorded daily until the numbers stabilized. From these data, angular transformation of final percentage germination (FPG) and days to 50% of FPG (G_{50}) were calculated. The experiment was a randomized complete block with 50 seeds per treatment and 5 replications (boxes) for the germination test.

Temperature and osmotic effects on germination. Nonprimed and primed tomato seeds that were surface-dried or dried-back were stored for 1.5 months at 4 or 20C. These seeds and nonstored surface-dried or dried-back primed seeds were germinated at 15, 25, or 35C in germination boxes containing two germination blotters moistened with 0.5-fold Hoagland solution without or with synthetic seawater to provide –0.05 MPa (low osmotic stress) and –0.40 MPa (high osmotic stress) at 25C, respectively. The 7 (seed treatments) × 2 (osmotic stress) × 3 (temperature) factorial in completely randomized-block design had five replications (50 seeds per box) for the germination assay. Ten replications of 100 seeds for each seed treatment were used to determine seed moisture content at the start and end of the storage period.

Results and Discussion

Seed storage duration. Primed asparagus seeds had lower G_{50} than nonprimed seeds (Table 1). The combination of surface-drying and 4C storage gave the lowest G_{50} value. Extending 4C storage of primed surface-dried seeds from 1 to 2 or 3 months

Table 1. Final percentage germination, days to 50% final percentage germination (G_{50}), and moisture content of osmotically primed asparagus seeds as affected by seed drying regime and seed storage duration and temperature.

Storage duration (mo.)	Seed treatment[z]	G_{50} (days) 4	G_{50} (days) 20	Final germination (% [angular transformation]) 4	Final germination (% [angular transformation]) 20	Seed moisture (%, w/w)[y] 4	Seed moisture (%, w/w)[y] 20
0[x]	NP	9.2 ± 0.8		89 ± 2 [71]		7.1 ± 0.5	
	PSD	5.4 ± 0.5		92 ± 3 [73]		49.4 ± 1.6	
	PDB	6.1 ± 1.2		91 ± 3 [73]		24.9 ± 2.4	
1	NP	9.6	9.3	89 [71]	89 [71]	8.8	6.1
	PSD	2.9	4.7	96 [79]	93 [76]	47.5	37.4
	PDB	5.8	7.0	92 [74]	89 [72]	20.1	18.9
2	NP	9.1	8.8	86 [68]	87 [69]	7.4	5.8
	PSD	1.4	6.0	93 [75]	87 [70]	44.8	26.2
	PDB	6.0	7.3	89 [71]	80 [64]	17.8	12.7
3	NP	9.1	9.2	91 [73]	87 [69]	7.3	6.1
	PSD	1.6	6.9	96 [79]	89 [71]	45.4	18.4
	PDB	7.3	7.4	85 [68]	86 [69]	11.2	7.4
	$LSD_{0.05}$[w]	0.2		[2]		0.6	
Significances (factorial treatments)							
Storage temp (T)		**		[**]		**	
Storage duration (D)		**		[**]		**	
Seed treatment (ST)		**		[**]		**	
T × D		**		[NS]		**	
T × ST		**		[NS]		**	
D × ST		**		[NS]		**	
T × D × ST		**		[NS]		**	

[z]Seed treatment: NP = nonprimed; PSD = primed and surface-dried; PDB = primed and dried-back.
[y]Wet weight basis, oven-dried (130C, 1 h).
[x]Nonstored seeds, mean ± SD (n = 5, except n = 10 for seed moisture content).
[w]$LSD_{0.05}$ applies to the three-way T × D × ST interaction.

Table 2. Final percentage germination, days to 50% final percentage germination (G_{50}), and moisture content of osmotically primed tomato seeds as affected by seed drying regime and seed storage duration and temperature.

Storage duration (mo.)	Seed treatment[z]	G_{50} (days) 4	G_{50} (days) 20	Final germination (% [angular transformation]) 4	Final germination (% [angular transformation]) 20	Seed moisture (%, w/w)[y] 4	Seed moisture (%, w/w)[y] 20
0[x]	NP	4.2 ± 0.1		95 ± 2 [78]		9.3 ± 0.6	
	PSD	1.7 ± 0.2		91 ± 4 [73]		46.6 ± 4.5	
	PDB	1.7 ± 0.2		92 ± 4 [74]		12.1 ± 1.2	
1	NP	4.1	4.1	95 [77]	95 [78]	8.5	9.3
	PSD	1.9	1.5	92 [75]	92 [73]	37.5	9.7
	PDB	1.9	1.9	93 [76]	91 [73]	11.5	10.5
2	NP	4.1	4.1	94 [78]	96 [78]	8.6	8.9
	PSD	2.0	1.8	90 [72]	87 [70]	20.7	8.6
	PDB	1.7	1.7	94 [76]	94 [76]	10.0	9.0
3	NP	4.2	4.1	94 [78]	96 [79]	7.2	7.7
	PSD	2.2	2.0	89 [71]	88 [70]	18.9	8.6
	PDB	1.8	2.0	93 [76]	93 [75]	8.2	8.0
	$LSD_{0.05}$[w]	0.2		[3]		0.6	
Significances (factorial treatments)							
Storage temp (T)		*		[NS]		**	
Storage duration (D)		**		[NS]		**	
Seed treatment (ST)		**		[**]		**	
T × D		NS		[NS]		**	
T × ST		**		[NS]		**	
D × ST		**		[NS]		**	
T × D × ST		NS		[NS]		**	

[z]Seed treatment: NP = nonprimed; PSD = primed and surface-dried; PDB = primed and dried-back.
[y]Wet weight basis, oven dried (130C, 1 h).
[x]Nonstored seeds, mean ± SD (n = 5, except n = 10 for seed moisture content).
[w]$LSD_{0.05}$ applies to the three-way T × D × ST interaction.

Table 3. Final percentage germination and days to 50% final percentage germination (G_{50}) of osmotically primed asparagus seeds at three temperatures and two osmotic stress levels as a result of seed drying regimes and storage for 0 or 1.5 months at 4 or 20C.

Germination environment		Seed treatment[z]							
Temp (C)	Osmotic stress[y]	NP	PSD	PSD4	PSD20	PDB	PDB4	PDB20	$LSD_{0.05}$[x]
		Final germination (% [angular transformation])							
15	low	88	78	96	66	50	77	54	
		[70]	[62]	[79]	[55]	[45]	[61]	[48]	[6]
	high	48	50	74	44	20	24	26	
		[44]	[45]	[60]	[41]	[26]	[29]	[30]	[6]
25	low	93	93	96	93	90	94	92	
		[75]	[75]	[80]	[74]	[71]	[77]	[73]	[6]
	high	94	97	95	92	88	88	90	
		[78]	[81]	[77]	[74]	[70]	[70]	[71]	[6]
35	low	57	75	82	70	72	71	75	
		[49]	[60]	[65]	[57]	[58]	[58]	[60]	[6]
	high	21	30	27	15	30	21	21	
		[27]	[35]	[31]	[22]	[35]	[26]	[26]	[6]
$LSD_{0.05}$ (three-way) = [8]									
		G_{50} (days)							
15	low	13.6	6.1	5.3	10.8	8.9	12.5	13.6	1.6
	high	17.4	8.5	8.6	13.5	9.8	18.5	16.3	3.8
25	low	6.2	2.5	2.7	4.0	3.8	4.8	5.7	0.5
	high	8.1	3.3	3.9	5.5	5.0	7.0	7.5	0.7
35	low	21.6	15.4	18.1	23.8	9.6	30.0	32.4	8.0
	high	26.8	46.9	27.1	18.3	8.3	40.0	42.8	11.3
$LSD_{0.05}$ (three-way) = 5.2									

F test significances[w]

	Final germination (angular transformation)	G_{50}
Germination temperature (T)	***	***
Osmotic stress (O)	*	***
Seed treatment (ST)	***	***
T × O	***	***
T × ST	***	***
O × ST	NS	***
T × O × ST	**	***

[z]Seed treatment: NP = nonprimed; PSD = primed and surface-dried, nonstored; PSD4 = primed and surface-dried, stored 1.5 months at 4C; PSD20 = primed and surface-dried, stored 1.5 months at 20C; PDB = primed and dried-back, nonstored; PDB4 = primed and dried-back, stored 1.5 months at 4C; PDB20 = primed and dried-back, stored 1.5 months at 20C.

[y]Osmotic stress: 0.5-fold Hoagland solution, without (low) or with (high) synthetic seawater to provide –0.382, –0.395 and –0.408 MPa at 15, 25, or 35C, respectively.

[x]$LSD_{0.05}$ applies to seed treatments within a temperature × osmotic stress regime.

[NS,***,**,*]Nonsignificant or significant at P = 0.001, 0.01, 0.05, respectively.

reduced G_{50} an average 1.4 days. Conversely, extending 20C storage from 1 to 3 months increased G_{50} of primed surface-dried seeds by 2.2 days.

Nonstored asparagus seeds (primed surface-dried, primed dried-back, or nonprimed) had similar FPG (Table 1). Surface-dried primed seeds had greater FPG than primed dried-back seeds, irrespective of storage temperature or duration. After 1-month storage at 4 or 20C, primed surface-dried seeds had slightly greater FPG than nonprimed seeds. After 2 or 3 months storage, however, only primed surface-dried seeds stored at 4C had greater FPG than nonprimed seeds.

Primed dried-back asparagus seeds had half the moisture of primed surface-dried seeds (24.9% vs. 49.4%) before storage (Table 1). While primed surface-dried seeds stored at 4C had 45% to 49% moisture, regardless of storage duration, the moisture of these seeds stored at 20C decreased from 49% to 18% as storage extended from 0 to 3 months (Table 1). Seed moisture of primed dried-back seeds was greater following storage at 4C rather than 20C, but decreased as storage duration increased.

The enhanced germination percentage and rate of primed surface-dried asparagus seeds, compared to germination of non-primed or primed dried-back seeds, after up to 3 months of storage at 4C was associated with high seed moisture (Table 1). Such cold-storage of high-moisture asparagus seeds may have provided an extension of the priming period, 4C being high enough for continued metabolism, but too low for radicle emergence. Surface-dried asparagus seeds stored at 20C had both decreased FPG with >1-month storage and increased G_{50} with increasing storage duration. These responses revealed deterioration of seeds stored at elevated temperature and moisture.

Primed tomato seeds had lower G_{50} values than nonprimed seeds (Table 2). Differences in G_{50} between surface-dried and

Table 4. Seed moisture of non-primed or surface-dried or dried-back primed asparagus and tomato seeds at the start and end of storage for 1.5 months at 4 or 20C.

		Seed moisture (%, w/w)z			
		Asparagus		Tomato	
Seed	Storage	Storage		Storage	
treatment	temp (C)	Start	End	Start	End
Nonprimed	4	10.2 ± 0.3	10.3 ± 0.4	10.6 ± 0.5	10.1 ± 0.5
	20	---	8.3 ± 0.3	---	8.1 ± 0.4
Primed and surface-dried	4	42.2 ± 1.0	40.3 ± 0.9	42.0 ± 1.8	36.7 ± 1.1
	20	---	27.4 ± 1.1	---	12.6 ± 2.0
Primed and dried-back	4	19.0 ± 3.1	16.6 ± 2.9	12.6 ± 0.9	12.0 ± 4.9
	20	---	12.9 ± 0.7	---	6.7 ± 0.4

zWet weight basis, oven-dried (130C, 1 h). Means ± SD, n = 20 at start of storage, n = 10 at end of storage.

dried-back primed seeds were too small to be of practical value. Increasing storage duration at 4C slightly increased the G_{50} of primed surface-dried tomato seeds, but had no effect on the G_{50} of primed dried-back or nonprimed seeds. Tomato FPG was unaffected by storage temperature or duration, but seed treatment had a slight effect (Table 2).

Primed surface-dried tomato seeds stored at 4C had more than twice the moisture of those stored at 20C, but storage temperature had little effect on the moisture content of primed dried-back or nonprimed seeds (Table 2). The moisture content of primed surface-dried seeds stored at 4C decreased from 47% (nonstored seeds) to 19% after 3 months storage. With 20C storage, seed moisture ranged only 2.8% as a result of seed treatment.

Even though primed surface-dried tomato seeds germinated more rapidly after storage than nonprimed seeds, the slightly lower FPG of these high moisture seeds (Table 2) revealed reduced storage life. Argerich et al. (1989) concluded that primed tomato seeds must be considered to be vigorous with reduced storage life.

Successful storage of primed seeds for 1 year or more usually requires drying the primed seeds to some low moisture content such as 6% for tomato (Alvarado and Bradford, 1988; Argerich et al., 1989). We know of no reports on high seed moisture content (≈45%) and refrigeration (4C) during storage of primed seeds, as was exhibited by asparagus seeds, exerting such a beneficial effect on subsequent germination rate without reducing viability.

Moisture was lost from primed seeds during storage despite seed containment in tightly-lidded metal cans which, in turn, were heat-sealed in plastic pouches. The moisture loss was more rapid from primed tomato seeds than from primed asparagus seeds, and was more rapid during 20C storage than 4C storage. We speculate that these differences in drying rates may be due, in part, to the lower specific surface of spherical asparagus seeds and to the lower vapor concentration needed to saturate the seed environment at 4C. Further work is required to evaluate the effect of container size on moisture retention of high-moisture primed seeds. Ibrahim et al. (1983) noted that while longevity of lettuce seeds under hermetic storage decreased with increasing seed moisture content, longevity increased exponentially up to 44% moisture content (close to full imbibition) in aerobic conditions. These authors suggested that in aerobic conditions, as afforded by the nonhermetic seed storage in our study, increased rate of normal metabolism associated with increased seed moisture could be sustained by respiration.

Temperature and osmotic effects on germination. High osmotic stress (–0.4 MPa) decreased asparagus FPG at 15 and 35C, but had no effect at 25C (Table 3). At 15C, only primed surface-dried seeds stored at 4C had greater FPG than nonprimed seeds, the benefit of this treatment being especially pronounced with high osmotic stress, with FPG increasing from 48% (nonprimed) to 74% (primed surface-dried). Conversely, primed dried-back asparagus seeds had lower FPG than nonprimed seeds at 15C. At 25C, seed treatment had no effect on FPG regardless of osmotic regime. At 35C with low osmotic stress, all priming treatments increased FPG compared with nonprimed seeds; but with high osmotic stress, only nonstored primed (surface-dried or dried-back) seeds had greater FPG than nonprimed seeds.

Primed surface-dried apsaragus seeds had lower G_{50} than nonprimed seeds when germinated at 15 or 25C, irrespective of osmotic regime (Table 3). Primed surface-dried seeds that were not stored or stored at 4C had the same G_{50}, but storing these seeds at 20C delayed germination, particularly at 15C. Compared to nonprimed seeds, nonstored primed dried-back seeds had lower G_{50} at 15 or 25C, but storing the dried-back seeds had little or no benefit on germination rate. Only nonstored primed dried-back seeds had lower G_{50} than nonprimed seeds germinated at 35C.

Moisture content of primed surface-dried asparagus seeds (42.2%) was more than twice that of primed dried-back seeds (19.0%) at the start of seed storage (Table 4). The moisture content of both primed surface-dried and primed dried-back seeds decreased only slightly after 1.5-month storage at 4C, but decreased considerably in 20C storage.

These results reveal the benefit of high-moisture primed asparagus seeds (surface-dried and stored at 4C) in increasing viability and germination rate under cool (15C) germination conditions, this response being more pronounced under high osmotic stress. Evans and Pill (1989) showed that field-emergence percentage and rate from primed asparagus seeds decreased when the seeds were dried before planting. Similarly, percentage and rate of seedling emergence was greater from $NaNO_3$-primed than from nonprimed asparagus seeds in a salinized seed bed in a glasshouse, provided the primed seeds were not dried-back (Pill et al., 1991). Priming of asparagus seeds conferred increased tolerance to high-temperature germination (35C, low osmotic stress) as revealed by the average 17%-point greater FPG of primed seeds compared to nonprimed seeds (Table 3). This benefit was maintained in the presence of high osmotic stress at 35C, but only when the primed seeds were not stored.

Primed and nonprimed tomato seeds had similar FPG when germination was assessed at 15 or 25C, irrespective of osmotic regime (Table 5). At 35C with low osmotic stress, all priming treatments greatly increased FPG, but primed seeds stored at 20C had slightly lower FPG than those stored at 4C. At 35C with high osmotic stress, FPG of any seed treatment was ≤5%. Pill et al. (1991) noted that primed tomato seeds had greater FGP than nonprimed seeds at 10C in both saline and nonsaline media. They noted further that while priming did not increase tomato FPG at 20C, priming osmoticum influenced FGP at 30C under saline conditions with $NaNO_3$ giving higher FGP than synthetic seawater.

Tomato G_{50} was increased by germination at 15C compared with 25C, and by high omsotic stress compared with low (Table 5). At 15 or 25C, seeds of all priming treatments had lower G_{50} than nonprimed seeds. Higher seed moisture following storage of primed seeds at 4C than at 20C (Table 4) was associated with lower G_{50} at 15 or 25C (Table 5). After 1.5-month storage, the moisturecontent of primed seeds had decreased, the decrease being

Table 5. Final percentage germination and days to 50% final percentage germination (G_{50}) of osmotically primed tomato seeds at three temperatures and two osmotic stress levels as a result of seed drying regimes and storage for 0 or 1.5 months at 4 or 20C.

Germination environment		Seed treatment[z]							
Temp (C)	Osmotic stress[y]	NP	PSD	PSD4	PSD20	PDB	PDB4	PDB20	$LSD_{0.05}$[x]
		Final % germination (angular transformation)							
15	low	97	94	90	92	97	92	89	
		[81]	[76]	[71]	[74]	[83]	[74]	[71]	[7]
	high	84	92	83	88	92	90	89	
		[67]	[73]	[66]	[71]	[75]	[72]	[70]	[9]
25	low	97	92	93	96	95	89	91	
		[83]	[74]	[75]	[79]	[79]	[71]	[72]	[10]
	high	92	92	90	90	92	85	86	
		[73]	[73]	[71]	[72]	[74]	[67]	[68]	[6]
35	low	2	57	56	35	45	50	39	
		[6]	[49]	[49]	[36]	[42]	[45]	[39]	[5]
	high	1	5	3	3	3	5	4	
		[2]	[13]	[8]	[8]	[10]	[13]	[11]	[3]
$LSD_{0.05}$ (three-way) = [7]									
		G_{50} (days)							
15	low	6.1	2.6	2.8	3.3	2.2	3.1	3.5	0.3
	high	10.3	6.0	6.1	7.3	5.9	5.3	7.3	1.1
25	low	2.7	0.8	1.0	1.3	0.9	0.7	1.0	0.2
	high	4.5	1.8	2.2	3.0	2.2	2.0	2.5	0.4
35	low	---[w]	0.7	0.7	0.8	0.7	0.8	1.1	0.3
	high	---	---	---	---	---	---	---	---
$LSD_{0.05}$ (three-way, excluding 35C) = 0.7									

F test significances

	Final germination (angular transformation)	G_{50}
Germination temperature (T)	NS	***
Osmotic stress (O)	***	***
Seed treatment (ST)	***	***
T × O	NS	***
T × ST	NS	***
O × ST	NS	**
T × O × ST	NS	NS

[z]Seed treatment: NP = nonprimed; PSD = primed and surface-dried, nonstored; PSD4 = primed and surface-dried, stored 1.5 months at 4C; PSD20 = primed and surface-dried, stored 1.5 months at 20C; PDB = primed and dried-back, nonstored; PDB4 = primed and dried-back, stored 1.5 months at 4C; PDB20 = primed and dried-back, stored 1.5 months at 20C.

[y]Osmotic stress: 0.5-fold Hoagland solution, without (low) or with (high) 160 mOsm synthetic seawater (–0.382, –0.395, or –0.408 MPa at 15, 25 ,or 35C, respectively).

[x]$LSD_{0.05}$ applies to seed treatments within a temperature × osmotic stress regime.

[w]G_{50} values incalculable owing to low percentage germination.

NS,***,**,*Nonsignificant or significant at P = 0.001, 0.01, or 0.05, respectively.

greater from surface-dried than from dried-back seeds, and with storage at 20C rather than 4C. Alvarado and Bradford (1989) attributed the more rapid germination from KNO_3-primed than from PEG-primed tomato seeds following 6-month storage to greater seed development due to higher seed moisture.

The promotive effects of low-temperature storage may be attributed to slowed seed deterioration and elevated seed moisture. Cold, moist storage of seeds following osmotic priming was similar to a low-temperature pre-sowing treatment used by Coolbear and McGill (1990), in which tomato seeds were soaked in distilled water at 10C for 21 days and then dried back to their original moisture contents. Seeds of this treatment had lower G_{50} at 10, 20, or 30C and higher FPG at 30C than untreated seeds.

The use of synthetic seawater to provide high osmotic stress during germination may have resulted in overpriming, a response noted in KNO_3-primed but not in PEG-primed seeds (Alvarado and Bradford, 1988). The higher seed moisture content of salt-primed seeds as a result of water influx along the steepened osmotic gradient caused the seed to reach a more advanced stage of development. Such seeds have increased susceptibility to desiccation and mechanical injury.

The results of these studies show that for maximal germination percentage and rate of primed seeds after up to 3 months of storage, both asparagus and tomato seeds should be held at 4C rather than 20C, but that the optimal drying regime for the primed seeds before storage was species specific. Primed asparagus seeds should be surface-dried and primed tomato seeds should be dried-back.

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