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Temperature and Seed Moisture Govern Germination and Storage of Gerbera Seed

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Abstract. **Temperature, relative humidity (RH), desiccation, and hydration affect gerbera (*Gerbera jamesonii* H Bolus ex Hook.f.) seed storage and germination. Germination percentages (G) were maximal and about equal at constant 15, 20, or 25C in darkness or light but lower at alternating temperatures having the same mean temperature. The number of days to 50% final germination (T_{50}) and between 10% and 90% germination ($T_{90} - T_{10}$) required the fewest days at constant 25 or 30C; longer germination periods resulted with alternating temperatures. Reducing seed moisture from 7.1% to 3.5% had no effect on G, T_{50}, or $T_{90} - T_{10}$ values, but at seed moisture levels <3.5%, G was lower and T_{50} and $T_{90} - T_{10}$ longer. Germination percentages were similar after seed storage from 5 to –5C, but G was lower after storage at –10C or lower. Low-temperature seed storage had no effect on T_{50} or $T_{90} - T_{10}$ values. Seeds had highest G and lowest T_{50} and $T_{90} - T_{10}$ values when germinated at 52% seed moisture, with large declines and delays in germination at lower and higher moisture levels. Seed storage for 12 months without reduction in germination was possible at 5C and 11% or 32% RH. Seeds stored at 52% RH lost G at all temperatures, and no seed germinated after storage at 75% RH and 15 or 25C. Seed stored at 5 or 15C and 11% to 32% RH had the fewest days to T_{50} and $T_{90} - T_{10}$.**

Plant breeders have developed gerbera strains for cut flowers, bedding and landscape plantings, and flowering pot plants. Gerbera are propagated primarily from seed, although meristem-tip culture procedures are commonly used by commercial micropropagation laboratories. Post (1949) recommended gerbera propagation by seed or division but provided no information for germinating seeds. Ball (1991) reported 21 to 24C as the optimum temperature range for germination and further suggested seeds be covered with finely shredded sphagnum peat. Our literature search found no other recommendations for seed storage or germination. Year-round propagation, production, and sale of plants has increased growers' need for more information on gerbera seed storage and germination. Our research objectives were to determine light, seed moisture, and temperature requirements during germination and to evaluate the effects of temperature, relative humidity (RH), and seed desiccation during seed storage.

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Materials and Methods

Seed handling and germination procedures. 'Painted Center Dark Eye' seeds, used in all our studies, were harvested by Earl J. Small Growers, Pinellas Park, Fla., on 14 Sept. 1992. After receipt on 30 Sept., seeds were dusted with 3α,4,7,7α-tetrahydro-2-[(trichloromethyl) thio]-1-*H*-isoindole-1,3 (2*H*) dione (captan). All treatments contained four 100-seed replications, each of which was germinated in individual 9-cm petri dishes on blue blotter paper 100 (Anchor Paper Co., Charlotte, N.C.) and moistened with 5 ml of distilled water (DW) unless otherwise designated. Germination studies were conducted in incubators (Stults Scientific Engineering Corp., Springfield, Ill.). In each study, germination counts were made daily of seeds with radicle protrusion through the testa. Total germination percentages (G), the number of days to 50% final germination (T_{50}) and between 10% and 90% germination ($T_{90} - T_{10}$) were calculated as described by Furutani et al. (1985).

Light and temperature studies. Imbibed seeds were kept in darkness or in continuous incandescent light at 15 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of photosynthetically active radiation in incubators at constant 15, 20, 25, 30, or 35C. In a second study, seeds were germinated in dark incubators with 12/12-h cycles at 10/20C, 15/25C, or 20/30C. The design for both studies was a randomized block with data analyzed separately for each study and combined for both studies by analysis of variance (ANOVA) and the fitting of linear and quadratic regression equations. Pairwise comparisons of mean values were performed using least significant difference (LSD) at $P \leq 0.05$.

Seed moisture content during storage. Seeds were weighed, placed in 9-cm open petri dishes, and dehydrated for 6, 12, 24, 48, or 72 h in 40C forced-draft ovens. Following dehydration, seeds of each replication were reweighed and immediately sealed in screw-capped, 10-ml, glass vials (100 seeds per vial) and stored at 5C for 4 weeks. After storage, seeds were reweighed and germinated at a constant 25C. Germination data were analyzed for seed moisture content by ANOVA, fitting linear and quadratic regression equations, and Tukey's HSD procedure. The initial

Table 1. The effect of constant or alternating temperatures on total germination (G) and the number of days to 50% germination (T_{50}) and between 10% and 90% germination ($T_{90} - T_{10}$) of 'Painted Center Dark Eye' gerbera seeds in darkness. Data are the means of four 100-seed replications during 21 days of germination.

Temp		Germination responses		
Regime	°C	G	T_{50}	$T_{90} - T_{10}$
Constant	15	86	4.8	3.1
	20	86	4.6	3.0
	25	84	3.1	2.4
	30	76	3.5	2.6
	35	11	4.7	4.4
Alternating	10/20 (15)[z]	60	9.6	9.1
	15/25 (20)[z]	68	5.8	5.0
	20/30 (25)[z]	79	4.6	2.4
$LSD_{0.05}$		4.7	0.4	0.5

[z]Mean alternating temperature.

Table 2. Coefficient estimates and coefficient of determination value (R^2) for the fitted regression equations relating total germination percentages (G), the number of days to 50% germination (T_{50}) and between 10% and 90% germination ($T_{90} - T_{10}$) to levels of constant and mean alternating temperature. Estimated response = $b_0 + b_1$ temperature + b_2 temperature^2, where b_0 is a constant and b_1 and b_2 are the linear effects.

Germination	Temp		Coefficient estimates			
response	Regime	Range (°C)	b_0	b_1	b_2	R^2
G	Constant	15–30	96.4	–0.6		0.73
	Constant	15–35	–77.5	16.5	–0.4	0.95
T_{50}	Constant	15–30	6.4	–0.1		0.66
	Constant	15–35	12.7	–0.7	0.01	0.70
$T_{90} - T_{10}$	Constant	15–30	6.6	–0.3	0.01	0.58
	Constant	15–35	8.7	–0.5	0.01	0.81
G	Alternating	(15)–(25)	29.8	2.0		0.90
T_{50}	Alternating	(15)–(25)	35.7	–2.5	0.05	0.98
$T_{90} - T_{10}$	Alternating	(15)–(25)	30.4	–1.9	0.03	0.99

seed moisture content was determined by weighing four 100-seed lots, which were dehydrated at 50C for 48 h, and reweighing the seed after it cooled to room temperature.

Cold tolerance of seed. Seeds were placed in 15 × 2.5-cm petri dishes on wire screens supported by segments of tubing 1 cm above a chemical desiccant. Constant 22% RH was maintained in the sealed petri dishes by adding 50 ml of saturated potassium acetate to the bottom of each dish (Copeland, 1976). Seeds were placed in a refrigerated incubator at 20C during the week of dehydration. Following dehydration, seeds were placed immediately in 10-ml, sealed, glass vials (100 seeds per vial) and immersed in polyethylene glycol-water (v/v) in controlled-temperature baths (Guy and Carter, 1984) for 7 days at 5, 0, –5, –10, –15, or –20C. Bath temperatures were lowered 3C per hour to final temperatures, and that temperature was maintained for 7 days. Then the temperature was increased 4C per hour to 10C. Following low- or subzero-temperature treatment, seeds were germinated at a constant 25C as previously described. G, T_{50}, and $T_{90} - T_{10}$ data were analyzed using ANOVA and the fitting of simple regression equations and compared by the LSD procedure.

Seed water content and germination. Seeds were germinated at 25C on blotter paper moistened with 2.5, 5.0, 7.5, or 10 ml DW. The design was a randomized complete block with data analyzed by ANOVA and the fitting of linear and quadratic regression equations. The study was repeated to determine the moisture content after seeds were imbibed with water for 24 h at each treatment. Seed replications were weighed, imbibed for 24 h, blotted dry, vacuum-aspirated for 15 min to remove remaining surface moisture, and reweighed. Next, seeds of each replication were placed in open petri dishes, dehydrated in forced-draft ovens at 50C for 48 h, and reweighed after the seed cooled.

Temperature and relative humidity interactions during seed storage. Immediately after harvest, seeds were dusted with captan and stored at 11%, 32%, 52%, or 75% RH and 5, 15, or 25C for 3, 6, 9, or 12 months. Humidity treatments were achieved as previously described, except saturated lithium chloride, magnesium chloride, magnesium nitrate, and sodium chloride solutions were used to achieve the desired RH levels. Incubators with refrigeration and heating capacities maintained constant 5, 15, or 25C during seed storage. After storage, seeds were germinated in petri dishes at constant 25C in darkness. ANOVA and response surface model fitting techniques using the SAS (1985) general linear model were used to analyze the data for G, T_{50}, and $T_{90} - T_{10}$. Within each storage temperature, a randomized complete-block design was used with a factorial treatment structure (four × four) between RH and storage period. Contour plots of the estimated germination surfaces were generated from the fitted regression models to graphically show the relationship between each of the germination responses and of storage period and RH at each of the three storage temperatures.

Results

Germination temperature. Over the range of 15 to 30C constant temperatures, G decreased linearly with increasing temperature; however, over the range of 15 to 35C constant temperatures, G behaved curvilinearly with increasing temperature (Tables 1 and 2). G increased linearly as the mean alternating temperature increased (Tables 1 and 2). G was higher ($P < 0.05$) at a constant 15, 20, or 25C than at the corresponding mean alternating cycles of 10/20C, 15/25C, or 20/30C, as determined by LSD. The T_{50} values were lower at 25 and 30C than at the other constant temperatures, and constant 15, 20, or 25C had lower ($P < 0.05$) T_{50} than the corresponding alternating temperatures (Table 1). The T_{50} values decreased with increasing constant temperature over the 15 to 30C range but behaved quadratically over the 15 to 35C range (Tables 1 and 2). Over the mean alternating temperatures, the T_{50} values behaved quadratically. The $T_{90} - T_{10}$ span was shortest (2.4 days) at 25C when constant or when it was the mean of alternating temperatures (Table 1). Over the constant and alternating temperature ranges, the $T_{90} - T_{10}$ values behaved quadratically (Table 2). At 15 and 20C, the $T_{90} - T_{10}$ spans were shorter ($P \leq 0.05$) at constant temperatures than at the corresponding mean alternating temperatures (Table 1).

Seed moisture tolerance. A quadratic decline in G occurred during storage as seed moisture content was reduced from 7.1% to 2.2% (Table 3). Pairwise comparisons among G showed no differences between 3.5% to 7.1% moisture levels, but G was lower at 3.0% and 2.2% levels than at 7.1% as determined by Tukey's HSD. The T_{50} declined quadratically as seed moisture levels were reduced. No differences were found when comparisons were made among T_{50} values at seed moisture levels from 7.1% to 3.5%, but T_{50} increased ($P \leq 0.05$) at 3.0% and 2.2% relative to 7.1% (Table 3). The $T_{90} - T_{10}$ spans increased quadratically as seed moisture levels declined. No differences were found among $T_{90} - T_{10}$ span from 7.1% to 3.5% seed moisture levels, but values increased as moisture levels decreased to <3.5%.

Seed cold tolerance. The 7.1% moisture content of recently harvested seeds was reduced to 5.1% during 7 days of storage at 11% RH and 20C before low-temperature treatment. Similar G occurred for this seed when stored at 5 to –5C, but G decreased slightly at lower storage temperatures (Table 4). No trends in T_{50} or $T_{90} - T_{10}$ values occurred from lowering the storage temperature from 5 to –20C (Table 4).

Water content during germination. G, T_{50}, and $T_{90} - T_{10}$ values increased quadratically during germination when the seed moisture content increased from 43.7% to 55.4% (Table 5). G increased from 18% to 82% as seed moisture increased from 43.7% to 51.7%, and G declined to 70% at 55.4% seed moisture content. Both T_{50} and $T_{90} - T_{10}$ values declined as seed moisture contents increased from 43.7% to 51.7%, indicating more rapid and uniform

Table 3. Effect of reduced seed moisture content during 28 days of storage at 5C on total germination percentages (G) and the number of days to 50% germination (T_{50}) and between 10% and 90% germination ($T_{90} - T_{10}$) of recently harvested gerbera seeds. Treatments contained four 100-seed replications germinated in darkness at 25C during 14 days. Results of tests for trends across moisture levels are indicated.

Seed desiccation duration (h)	Moisture (%)	Germination responses G	T_{50}	$T_{90} - T_{10}$
0	7.1	83	3.1	2.4
6	5.7	81	3.0	2.4
12	4.2	81	3.0	2.4
24	3.5	80	3.0	2.8
48	3.0	70	3.5	3.8
72	2.2	63	4.7	5.0
Significance				
Linear		***	***	***
Quadratic		***z	***y	***x
$HSD_{0.05}$		5.0	0.4	0.6

zG = 30.5 + 18.6 m – 1.6 m²; R^2 = 0.85.
y$T_{50} = 7.8 - 1.9\ m + 0.2\ m^2$; $R^2 = 0.82$.
x$T_{90} - T_{10} = 9.5 - 2.6\ m + 0.2\ m^2$; $R^2 = 0.91$.
***Significant at $P \leq 0.001$.

Table 4. Effect of temperature on total germination percentages (G), and the number of days to 50% germination (T_{50}) and between 10% and 90% germination ($T_{90} - T_{10}$) of gerbera seed after low-temperature storage for 7 days at 5.1% moisture content. Data are the means of 400 seeds germinated in darkness at 25C during 14 days. Results of tests for trends across temperature levels are indicated.

Temp (°C)	Germination responses G	T_{50}	$T_{90} - T_{10}$
5	89	3.1	2.2
0	88	3.0	2.2
–5	87	3.2	2.2
–10	83	2.9	2.3
–15	83	2.9	2.0
–20	82	2.9	2.0
Significance			
Linear	*	NS	NS
$LSD_{0.05}$	4.2	0.2	0.3

NS, *Nonsignificant or significant at $P \leq 0.05$.

Table 5. Effect of moisture content on total germination percentages (G) and the number of days to 50% germination (T_{50}) and between 10% and 90% germination ($T_{90} - T_{10}$) of gerbera seed. Data are the means of 400 seeds germinated at 25C during 14 days. Results of test for trends across moisture levels are indicated.

Substrate water (ml)	Seed moisture (%)	Germination responses G	T_{50}	$T_{90} - T_{10}$
2.5	43.7	18	5.1	4.2
5.0	47.1	47	3.4	2.5
7.5	51.7	82	3.0	2.1
10.0	55.4	70	3.2	2.8
Significance				
Linear		***	***	***
Quadratic		**z	**y	**x

zG = 1993.3 + 78.5 m – 0.7 m²; R^2 = 0.93.
y$T_{50} = 92.2 - 3.45\ m + 0.03\ m^2$; $R^2 = 0.95$.
x$T_{90} - T_{10} = 45.9 - 1.79\ m + 0.02\ m^2$; $R^2 = 0.69$.
**, ***Significant at $P \leq 0.01$ and 0.001, respectively.

germination. The estimated minimum T_{50} value was 2.8 days at 51.8% seed moisture content, and the estimated minimum $T_{90} - T_{10}$ was 2.0 days at 49.1%. These estimated minimums were calculated from the quadratic equations footnoted in Table 5.

Storage temperature and RH. Drawing on inferences from the fitted regression equations (Table 6) and surface contour plots (Fig. 1) generated from the fitted models, total G decreased at all temperatures as RH levels increased >32% and storage periods lengthened from 6 to 12 months (Fig. 1 A–C). No seeds germinated after 3 to 12 months storage at 15 or 25C and 75% RH (hence the shaded regions in Fig. 1 B, C, E, F, H, and I). At 15C, G declined from 75% to 60% as storage increased from 3 to 12 months and RH increased from 32% to 52% and from 70% to 30% at 25C (Fig. 1 B and C). Similar G occurred after seed storage at 11% and 32% RH, with both having >80% G after 12 months storage at 5C compared to 75% and 70% G after 12 months storage at 15 and 25C, respectively. Maximum estimated germination was 82.2% for seeds stored 9 months at 22% RH and 5C.

The lowest T_{50} resulted after 9 months of

Table 6. Coefficient estimates and coefficient of determination (R^2) values for the fitted regression models in Fig. 1. Estimated response = $b_0 + b_1SP + b_2RH + b_3SP \times RH + b_4SP^2 + b_5RH^2 + b_6SP \times RH^2$ (SP = storage period; RH = relative humidity; b_1 and b_2 = linear effects, b_4 and b_5 = quadratic effects, and b_3 and b_6 = interactive effects).

	Temp	Coefficient estimates								
Response	(°C)	b_0	b_1	b_2	b_3	b_4	b_5	b_6	R^2	Figure
G	5	76.79	–0.31	–0.03	0.09		7.2×10^{-4}	-1.9×10^{-3}	0.872	1A
	15	87.55	–2.02	–0.76	0.17		1.3×10^{-2}	-3.3×10^{-3}	0.659	1B
	25	79.26	–3.12	0.07	0.21		2.0×10^{-3}	-5.2×10^{-3}	0.878	1C
T_{50}	5	3.44	–0.12	–0.02	1.1×10^{-3}	4.5×10^{-3}	2.3×10^{-4}		0.700	1D
	15	4.29	–0.21	–0.06	2.1×10^{-3}	8.6×10^{-3}	8.2×10^{-4}		0.806	1E
	25	3.37	–0.08	-9.9×10^{-3}	-5.3×10^{-3}	8.1×10^{-3}	3.4×10^{-4}	1.1×10^{-4}	0.900	1F
$T_{90} - T_{10}$	5	3.54	–0.20	–0.06	6.1×10^{-3}	2.3×10^{-3}	5.6×10^{-4}	-5.2×10^{-5}	0.458	1G
	15	5.61	–0.63	–0.18	2.8×10^{-2}	2.1×10^{-3}	-1.9×10^{-4}	-1.9×10^{-4}	0.611	1H
	25	1.98	-0.09	0.05	-9.5×10^{-3}	1.2×10^{-2}	-6.9×10^{-4}	1.9×10^{-4}	0.844	1I

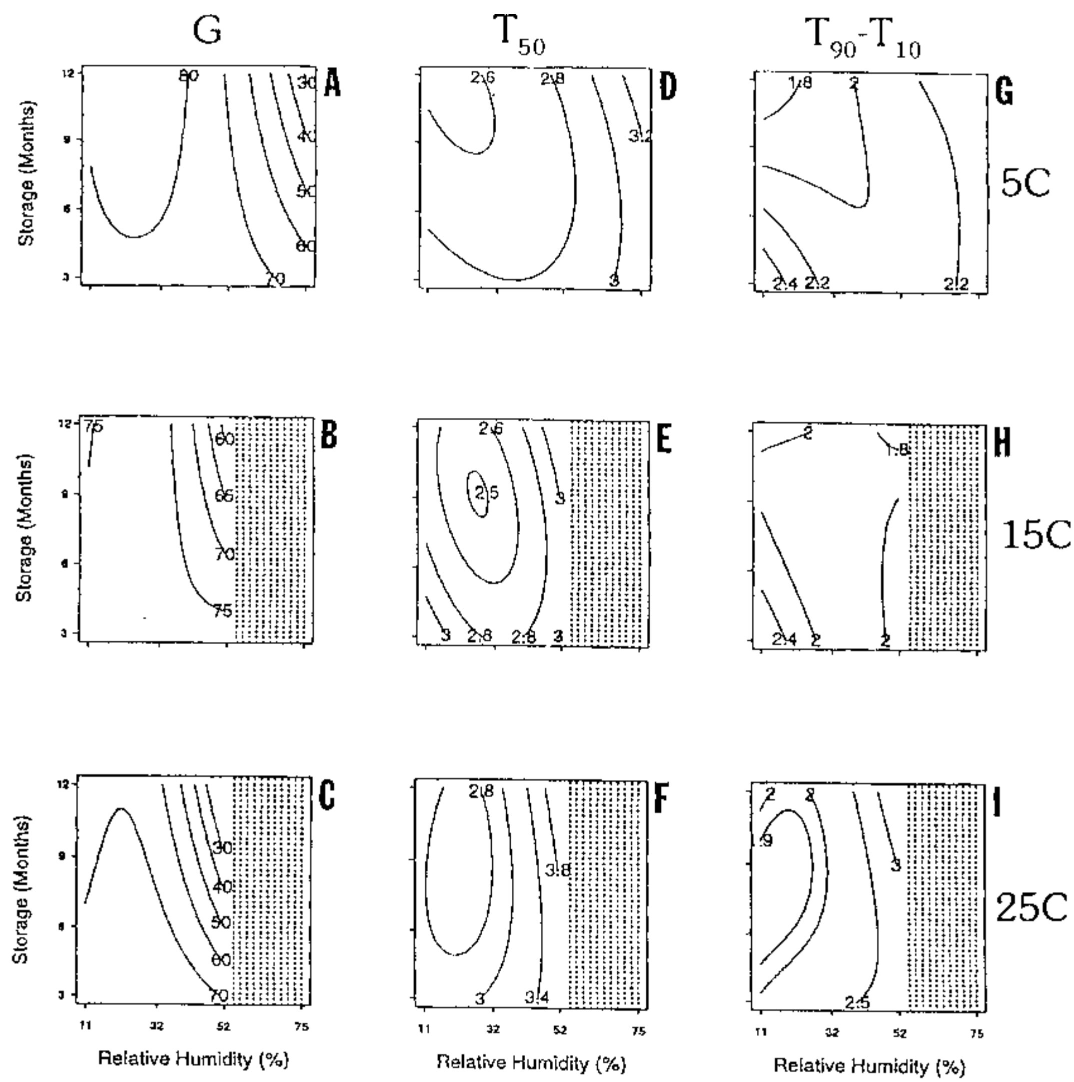

Fig. 1. (**A–C**) Contour plots for the total germination percentages (G), and (**D–F**) the number of days to 50% germination (T_{50}) and (**G–I**) between 10% and 90% germination ($T_{90} - T_{10}$) for gerbera seeds germinated at 25C in darkness following storage at 11% to 75% relative humidity for 3 to 12 months at (**A, D, G**) 5, (**B, E, H**) 15, or (**C, F, I**) 25C. Regression equations used to generate these plots are listed in Table 6. (**B–I**) The shaded regions signify that no seeds germinated after storage at >52% RH at 15 or 25C.

storage at 32% RH or 15C (Fig. 1E). Seeds stored at 5 or 15C and 11% to 32% RH required 2.6 to 2.8 days for T_{50}, but 2.8 to 3.0 days were required after storage at 25C (Fig. 1D–F). The longest delay in T_{50} was after seed storage at 25C and 52% RH; seed failed to germinate after storage at 75% RH and 15 or 25C. The spans in $T_{90} - T_{10}$ were similar (≤2.5 days) for seeds stored at 11% and 32% RH levels at all temperatures (Fig. 1G–I).

Discussion

Gerbera seed germination can be optimized by manipulating the environmental conditions during storage. Similar G, T_{50}, and $T_{90} - T_{10}$ were found in darkness or continuous light at 15 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at 25C (data not presented). Uniform G occurred at constant 15, 20, or 25C, which is a broader optimum temperature range than the ones recommended by Ball (1991) or Cathey (1976). Higher G and shorter T_{50} or $T_{90} - T_{10}$ values resulted at constant 15, 20, or 25C compared to alternating 12/12-h cycles of 10/20C, 15/25C, or 20/30C with corresponding means. Bewley and Black (1982) reported that alternating daily temperatures delayed the germination of seed not requiring low temperatures to terminate seed dormancy. Carpenter and Ostmark (1988) and Carpenter et al. (1991) reported that amaryllis (*Hippeastrum ×hybridum* Hort.) and gladiolus (*Gladiolus grandiflorus* Andr.), species lacking seed dormancy, had maximum G at optimum constant temperatures and significantly lower levels at 12-h alternating temperatures.

Improved practices and technology in the seed production industry have promoted the drying of freshly harvested seeds to low moisture levels for storage and shipment in sealed packages. It is important to know if excessive drying causes losses in seed viability or vigor. Our study showed that a significant decline in G occurred when the 7.1% moisture content of gerbera seeds at harvest was allowed to decline to <3.5% during storage, and the T_{50} and $T_{90} - T_{10}$ increased at seed moisture ≤3.5% and 4.2%, respectively. These results indicate the importance of controlling and limiting the moisture loss from the seed. Justice and Bass (1978) reported that delayed and irregular germination are the first indicators of injury from excessively low seed moisture contents during storage.

Bewley and Black (1982) reported that seed at moisture contents <14% do not form ice crystals within the cells when stored at <0C. Justice and Bass (1978) found subzero temperatures were best for long-term seed storage; the seed respiration rate is low at <0C. *Delphinium ×cultorum* Voss seed had no loss in total germination or vigor after storage for 5 years at –15C (Barton, 1932). In our study, gerbera seed with 5.1% moisture had no loss in G after storage from –5 to 5C, but G was lower after storage at –10C or lower (Table 3). T_{50} and $T_{90} - T_{10}$ were unchanged after seed storage at –20 to 5C for 7 days, indicating that gerbera seeds are relatively cold tolerant. Carpenter and Boucher (1992) found that reduced G and delayed and irregular germination of vinca [*Catharanthus roseus* (L.) G. Don] seed occurred after storage at subzero temperatures.

Seed moisture content during the 12-month storage study had a major effect on germination. The highest G and lowest T_{50} and $T_{90} - T_{10}$ values occurred after storage at 5C and 11% or 32% RH for seeds having 4.5% and 5.8% moisture content, respectively. Seeds stored at 5C and 75% RH had 7.9% moisture content, and G declined from 85% to 30% during 12 months of storage. No seeds germinated after 3 months of storage at 15 or 25C and 75% RH when seed moisture was 8.2% and 8.4%, respectively. Gerbera seed tolerated low moisture contents during storage but not levels higher than at seed harvest. Bewley and Black (1982) reported that seed deterioration rate during storage depends on the seed water content and temperature and is associated with the rate of food metabolism and respiratory activity. Species having nondormant seeds when shed from the mother plant and that can germinate over a wide temperature range have the most rapid deterioration when stored at high moisture levels (Justice and Bass, 1978).

Seeds of most species have the highest G between 35% and 60% moisture content. Copeland (1976) reported that the optimum seed moisture percentages for germinating corn (*Zea mays* L.), pea (*Pisum sativum* L.), soybean [*Glycine max* (L.) Merrill], and wheat (*Triticum aestivum* L.) were 32%, 60%, 51%, and 41%, respectively. Carpenter and Maekawa (1991) found 60% moisture content was optimum for 'Romance Scarlet' verbena (*Verbena ×hybrida* Voss) seed germination, with rapidly declining G at <56% and >63% moisture. Gerbera seed moisture during germination governed the G, T_{50}, and $T_{90} - T_{10}$ values. Maximum G (82%) was at 52% seed moisture, with 47% G at 47% moisture (Table 4). These results indicate that gerbera seeds have a narrow moisture tolerance range for best germination. The seeds required free water in the germination substrate to achieve 52% moisture content, but higher levels reduced G. Differences in seed moisture content during germination could contribute to variability in G and the irregular rates of germination reported by commercial producers.

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