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Germination of warm-season grasses under constant and dynamic temperatures

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Abstract

Fifteen collections of 10 native and exotic grasses were germinated at constant 25°C, and at gradual and abruptly alternating temperature regimes characteristic of wet seedbed temperatures in the southwest desert grassland in summer, winter, and spring. All species but bristlegrass (*Setaria macrostachya* H.B.K. and *S. leucopila* Schum.) had high total germination under summer and spring temperatures (mean= 60% and 67%, respectively) and all but bristlegrass and bush muhly (*Muhlenbergia porteri* Scribn.) had relatively high total germination under winter temperatures (mean=53%). In general, total germination percentage was similar for gradual and abruptly alternating temperature regimes within a season. Constant 25°C and abruptly alternating temperature germination percentages were similar enough to those at more realistic gradually alternating temperatures for most species to permit use of these tests to calculate estimates of summer bulk seeding rates. Time to 50% germination (D50) was slightly less for gradual than abruptly alternating summer temperatures, but was generally similar for these regimes under winter and spring temperatures. To determine if germination responses to constant temperatures could be used to estimate responses to dynamic temperatures, 12 collections of 8 species were tested for germination at constant temperatures of 5.4, 10, 20, 25, 30, 35, 40, and 45°C. Total germination and rate of germination (1/D50) increased and decreased as third-order polynomial functions of temperature. Polynomial regression estimates of 1/D50 were used to calculate estimates of D50 for diurnally alternating temperatures that were within an average of 0.6 and 1.3 days of measured values for summer and spring temperatures, respectively. Linear regression estimates of 1/D50 for suboptimal to optimal temperatures were similarly used to estimate D50 for dynamic winter temperature regimes that averaged within 3.6 days of measured values for most of the species. Differences between estimated and measured D50 for bush muhly under winter temperatures, and for Lehmann lovegrass (*Eragrostis lehmanniana* Nees) collections under winter and spring temperatures, indicate sensitivity of these species to extreme temperatures in addition to accumulated heat. Similar measured and estimated D50 for most of the collections for summer, winter, and spring temperatures indicates that these species are primarily responding to cumulative heat effects. Even though most of the species have high germination percentages for winter or spring temperatures, field seedling emergence is much less likely in winter and possibly less likely in spring than in summer. Slower germination rates during these cooler seasons would require long periods of soil water availability at the surface to allow germination.

Key Words: revegetation, modeling seedling establishment, semidesert grasslands, *Bothriochloa, Bouteloua, Digitaria, Eragrostis, Heteropogon, Leptochloa, Muhlenbergia, Setaria.*

Laboratory germination tests are used to calculate pure live seed percentages and bulk seeding rates, as well as to understand establishment requirements of rangeland species. The standards set forth by the Association of Official Seed Analysts (Yaklich 1984) recommend constant or abruptly alternating temperatures for germination trials, depending on the species. However, field seedbed temperatures diurnally rise and fall gradually (Roundy et al. 1992b). Differential germination responses to laboratory and actual field temperature patterns may limit the use of laboratory data for predicting or understanding seedling establishment under field conditions. Field germination responses may be important in understanding why certain exotic species, such as Lehmann and Cochise lovegrass (*Eragrostis lehmanniana* Nees and *E. lehmanniana* Nees x *E. trichophora* Coss and Dur.) are more easily established than some southwestern native grasses (Roundy and Biedenbender 1995).

Temperature patterns affect germinability of dormant seeds as well as the germination rate of nondormant seeds. Temperature alternations stimulate germination of many dormant seeds depending on the timing, number of cycles, extremes, and amplitude of the alternations (Murdock et al. 1989, Probert et al. 1986, Totterdell and Roberts 1980). Early (Wilson 1931, Little 1937, Bridges 1941) and more recent research (Munda 1993, Livingston 1992) has shown many native southwestern warm-season grasses to have high germination percentages and limited dormancy. Exceptions include plains lovegrass (*Eragrostis intermedia* Hitchc.), which had increased germination when exposed to alternating temperatures (Roundy et al. 1992c), and bristlegrass (*Setaria macrostachya* H.B.K., S. *leucopila* Schum.), which may require scarification to decrease seed coat dormancy (Tapia and Schmutz 1971). Collections of Lehmann lovegrass seed have dormancy that decreases with time, scarification, exposure to light, or various moisture and temperature pretreatments (Knipe

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and Herbel 1960, Brauen 1967, Haferkamp et al. 1977, Hardegree and Emmerich 1991, Roundy et al. 1992a, 1992c).

Germination rate at suboptimal temperatures increases linearly with increasing constant temperatures for nondormant seeds of many species (Hegarty 1972). This relationship has led to the use of accumulated thermal units above a base temperature to predict germination in time (Roberts 1988, Probert 1992), and is the basis for modeling seedling establishment in relation to periods of water availability (Brar et al. 1992). Following this approach, Jordan and Haferkamp (1989) used linear regression of constant temperatures on the reciprocal of days to 50% germination to estimate minimum germination temperatures of 7.8 to 13.7°C for native and exotic grasses common to southern Arizona. They calculated thermal units required to reach 50 % germination by subtracting these minimum temperatures from each constant or mean daily temperature to determine thermal units/day.

However, germination rates estimated from thermal units based on seed germination at constant or average temperatures could vary with those of seeds exposed to field temperature alternations. Garcia-Huidobro et al. (1982) found that nondormant seeds of pearl millet (*Pennisetum typhoides* S.&H.) required fewer thermal units to reach 50% emergence when the amplitude of temperature alternations was increased. Germination rates of seeds exposed to abrupt alternations between diurnal extremes, as is common with laboratory tests, might be negatively affected by the longer daily exposure of seeds to supraoptimal temperatures than would occur with the gradual temperature alternations of field conditions. Ellis et al. (1987) demonstrated a predictable decreasing germination response of faba bean (*Vicia faba* L.) to increasing temperatures above the optimal temperature for germination. Similar responses have been shown for other species (Roberts 1988). The purpose of our research was to compare germination responses of warm-season grasses at abruptly and gradually fluctuating temperatures and to determine if response to constant temperatures can be used to predict germination rates under dynamic temperature regimes.

Methods and Materials

Fifteen native and exotic warm-season perennial grass collections of 10 species (Table 1) were tested for total germination percentage and days to 50% germination of germinating seeds (D50) in relation to 7 temperature regimes. These regimes included constant 25°C; abruptly alternating temperatures between 20 and 40, 2 and 33, and 1 and 16°C, representing minimum and maximum wet seedbed temperatures in summer, spring, and winter, respectively, in the desert grassland in southern Arizona. Also tested were gradual diurnal fluctuating temperatures for these ranges, representing measured temperature patterns in wet field seedbeds (Fig. 1). Field seedbed temperatures for summer were measured by Sumrall et. al (1991), Roundy et al. (1992b), and in the current study for summer, winter and spring on a sandy loam upland range site using thermocouples attached to microloggers. Abruptly alternating trials were conducted in incubators set at the cooler temperature for 16 hours and the warmer temperature for 8 hours. Gradually fluctuating trials were held in a ramping temperature incubator, programmed to simulate diurnal measured field temperatures. In addition, germination percentage and D50 were measured for 12 collections of 8 species in constant temperature incubators at temperatures of 5.4, 10, 20, 25, 30, 35, 40, and 45°C.

For all germination tests, 4 replications of 25 seeds of each collection were placed in petri dishes lined with Watman #2 filter paper. Germination was recorded and dishes rotated in the incubators daily for up to 21 days, then every 3 days for up to 42 days. Seeds were counted as germinated when the radicle emerged 1-2 mm.

Analysis of variance was used to determine significance of collection, season, and temperature regime in relation to total germination percentage and D50. Collection and temperature regime means were separated by the Tukey HSD test. Germination percentages and the inverse of D50 were statistically fit to constant temperatures using linear and polynomial regression. Regression equations for each collection were used to estimate hourly values for the inverse of D50 for gradual and abruptly alternating temperature regimes. The inverse of progress toward 50% germination (1/PTG) for each hour was calculated by:

$$1/PTG/hour = estimated\ 1/D50\ /24$$

Daily 1/PTG was calculated by summing the hourly 1/PTG's for 24 hours. Estimated D50 was then calculated as the inverse of the daily 1/PTG for each collection and temperature regime.

Table 1. Species list for laboratory germination study of warm-season grasses including seed source and year collected.

Common name	Scientific name and lot #	Seed source and year
Cane beardgrass	*Bothriochloa barbinodis* Herter	TPMC[1]; harvested 1990, 1992
Sideoats grama	*Bouteloua curtipendula* (Michx.) Torr.'Vaughn' Lot 9221	Native Plants, Inc., Arizona; collected by 1986
Arizona cottontop	*Digitaria californica* (Benth.) Chase Lot 11175	Granite Seed Co., Utah; Arizona orig.;collected by 1991
Plains lovegrass	*Eragrostis intermedia* Hitchc.	Native Plants, Inc., Arizona; collected 1991
Lehmann lovegrass	*Eragrostis lehmanniana* Nees Lot 2814	Native Plants, Inc., Arizona; collected by 1987
	Lot 9178	Native Plants, Inc., Arizona; collected by 1986
	Lot 9247	Native Plants, Inc., Arizona; collected by 1987
Cochise lovegrass	*E. lehmanniana* Nees x *E. trichophora* Coss and Dur.	Unknown origin
	Lot 9366	Native Plants, Inc., Arizona; collected by 1988
Tanglehead	*Heteropogon contortus* (L.) Beauv.	TPMC; harvested 1991
Green sprangletop	*Leptochloa dubia* (H.B.K.) Nees Lot 113669	Granite Seed Co.; Texas orig.; collected by 1992
Bush muhly	*Muhlenbergia porteri* Scribn.-Arizona	Collected Tucson, Arizona; 1990
	New Mexico	Collected Jornada Expt. Range, New Mexico; 1991
Bristlegrass	*Setaria leucopila* Schum.	TPMC; harvested 1991
Plains bristlegrass	*Setaria machrostachya* H.B.K. Lot 11639	Granite Seed Co., Utah; Texas orig.;collected by 1992

[1]T PMC = Natural Resource Conservation Service, Tucson Plant Materials Center.

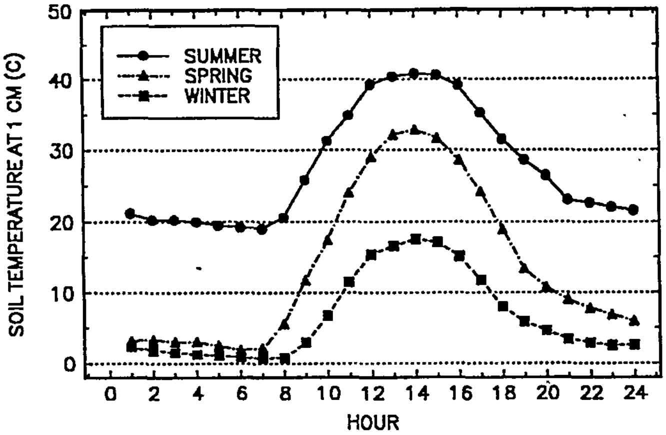

Fig. 1. Summer, spring, and winter wet seedbed temperatures in the desert grassland of southeastern Arizona.

Results

Response to Gradual and Abrupt Temperatures

The interaction of species, season, and temperature regime was significant (p>0.05) for total germination percentage and D50. In general, total germination was similar for constant 25°C, gradual, and abrupt temperature regimes for summer and spring temperatures (10 and 9 of 15 collections, respectively) (Table 2). Total germination responses to winter temperatures varied with species and collection. Constant, gradual, and abrupt temperature regimes had similar germination for 5 of 15 collections, while germination in abrupt and gradual temperatures was similar for 6 of 15 collections. Abruptly alternating winter temperatures stimulated germination of Lehmann lovegrass 9247 compared to constant or gradual temperatures. Germination in abrupt winter temperatures was less than that in gradual temperatures for 2 species, cane beardgrass and Arizona cottontop. Except for bristlegrass at all temperatures and bush muhly under winter temperatures, all native species had high germination percentages.

In general, germination was faster in gradual than in abrupt temperature regimes for summer temperatures (8 of 15 collections), but was similar for these temperature regimes for winter and spring temperatures (10 and 9 of 15 collections, respectively) (Table 3). As expected, germination was faster at a constant 25°C than in gradual and abruptly alternating winter temperature regimes for all collections. D50 was similar among most species and collection within gradual and abrupt summer temperature regimes. Germination was especially fast for summer gradual temperatures, with 50% germination occurring within 1.4 to 3.7 days of wetting. For winter temperatures, bush muhly and the Lehmann lovegrass collections had slower germination than the other collections. Germination rate was similar for all collections but bristlegrass under spring gradual temperatures. Under gradual temperatures, D50 was about 2 to 3 times longer under spring and 4 to 18 times longer under winter temperatures as under summer temperatures. Many native species had a trend toward faster germination than Lehmann lovegrass under spring and winter temperatures. Bush muhly was especially sensitive to cold temperatures.

Response to Constant Temperatures

Total germination percentage and 1/D50 increased with increasing constant temperatures to a point and then decreased. This response was best statistically modeled by third order polynomial regression equations (Fig. 2, Table 4). Optimum temperature for total germination for most collections was about 20°C, but was 30°C for plains lovegrass and bush muhly. Sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.] had highest total germination at the temperature extremes of 5.4 and 45°C, but

Table 2. Total germination percentage for 15 warm-season grasses under constant, gradual, and abruptly alternating temperatures representative of wet seedbed conditions in a southeastern Arizona desert grassland.

	Summer			Winter			Spring		
Species	Constant[1]	Gradual	Abrupt[2]	Constant	Gradual	Abrupt	Constant	Gradual	Abrupt
	Total Germination (%)								
Cane beardgrass	88aA[3]	80aAB	76aA-C	93aA	92aA	56bA-C	93aA	86abA	69bA-C
Sideoats grama	81aA-C	62bBE	48bD-F	81aA-C	80aAB	77aA	79aA-C	74aA-C	69aA-C
Arizona cottontop	64aCD	51abCE	32bF	64aCD	47aCD	23bD	61aB-D	56aB-D	56aC
Tanglehead	75aB-D	40bEF	81a A-C	68aB-D	66aBC	62aA-C	85aAB	79aAB	77aA-C
Green sprangletop	78aB-D	76aAB	69aB-D	70aB-D	67aBC	62aA-C	81aA-C	72aA-C	69aA-C
Bush muhly									
Arizona	64aDE	66aBD	61aB-E	48aDE	0bH	1bF	73aA-C	36bD	57abC
New Mexico	83aA-C	77aAB	92aA	84aA-C	1cGH	16bDE	92aA	81abAB	73bA-C
Bristlegrass	12aF	11aG	8aG	11aF	15aEF	1bF	12aF	7aEF	12aD
Plains bristlegrass	5aF	0aG	4aG	8aF	15aFG	4aEF	12aF	5aF	7aD
Plains lovegrass	87aAB	89aA	84aAB	87aAB	46bCD	62bA-C	87aAB	86aA	92aA
Lehmann lovegrass									
2814	63aCD	52aC-E	70aB-D	62aCD	51aB-D	68aA	52aC-E	72aA-C	86aAB
9178	48aEF	28bFG	58aC-E	28aEF	21aDF	39aB-D	34bD-F	47bCD	75aA-C
9247	38aF	10bG	40aEF	17bF	9bF-H	66aAB	24bEF	29bD	80aA-C
Cochise lovegrass									
6308	87aA-C	73aA-C	73aB-D	82aA-C	41bC-E	63aA-C	75aA-C	70aA-C	65aBC
9366	57aDE	45aD-F	43aEF	51aDE	23bD-F	35abCD	58aCD	26bDE	48abC

[1]Constant temperature was 25°C.
[2]Abruptly alternating temperature regimes remained at the cooler temperature for 16 hours and at the warmer temperature for 8 hours. Summer temperatures were 20-40; winter 1-16; and spring 2-33°C.
[3]Germination means among temperature regimes within a season for each seed collection followed by the same lower case letter and among seed collections within a column followed by the same upper case letter are not significantly different (p<0.05) by the Tukey HSD test.

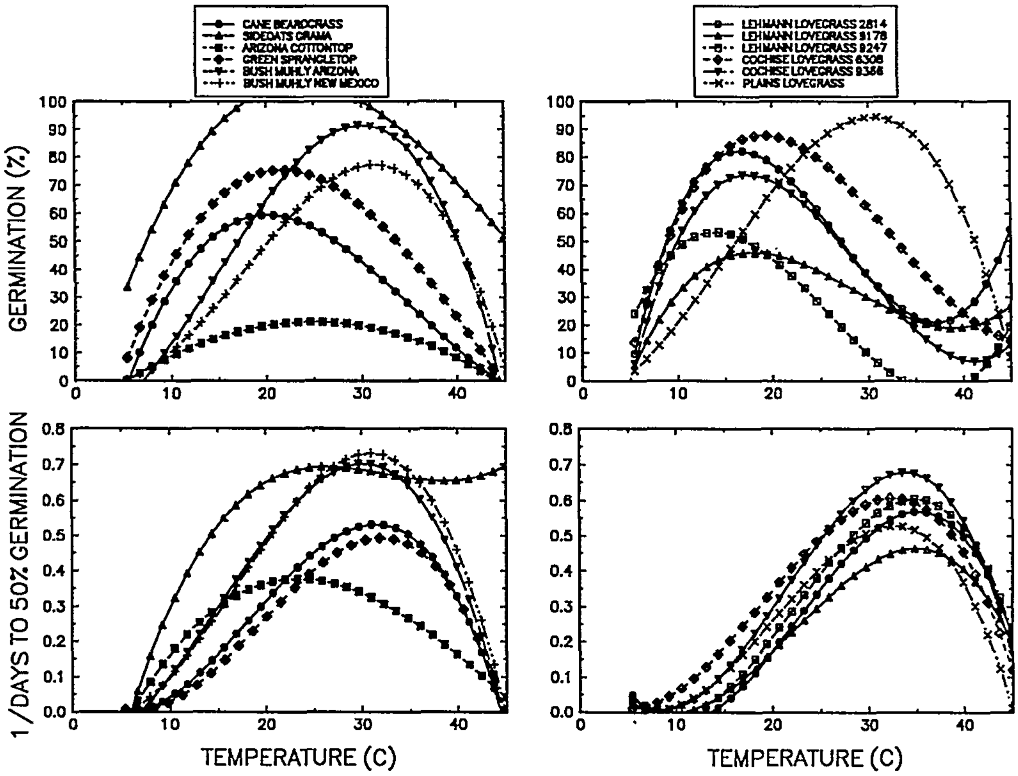

Fig. 2. Total germination and germination rate of warm-season grasses as third-order polynomial regression functions of constant temperature.

most native species had little or no germination at these temperatures. The Lehmann lovegrass collections had decreasing germination from 20 to 35 or 40°C, and then increased slightly at 45°C. Arizona cottontop's [*Digitaria californica* (Benth.) Chase] low germination percentage in the constant temperature trials may have been associated with loss of viability associated with seed age.

Most collections had rapid germination (greatest 1/D50) at 30 to 35°C and then decreasing germination rate at higher temperatures (Fig. 2). Sideoats grama had rapidly increasing germination rate with increasing temperature from 5.4 to 20°C and relatively constant germination rate at 20°C to 45°C. The introduced lovegrasses all had most rapid germination at 35°C. Optimum temperatures for total germination were generally 5 to 10°C cooler than those for maximum germination rate for native grasses and 15 to 20°C cooler for the introduced lovegrasses.

Estimating Germination Time

All polynomial regressions of 1/D50 on constant temperatures were significant ($p<0.001$), but standard errors of the estimate were relatively large (Table 4). Nevertheless, D50 estimates from this statistical model were similar to measured values for summer and spring temperature regimes for most collections (Fig. 3). For summer gradual temperatures, absolute differences between measured and estimated values ranged from 0.11 days for sideoats grama to 2.6 days for Cochise lovegrass 9366, and averaged 0.7 days. Estimated and measured values of D50 were more similar for abrupt than gradual summer temperatures. Differences between measured and estimated values for this regime averaged only 0.4 days. For summer temperature regimes, the model generally overestimated D50 for gradual temperatures and underestimated D50 for abrupt temperatures. Differences between estimated and measured D50 for gradual spring temperatures ranged from 0.06 to 2.9 days and averaged 1.1 days. Differences between estimated and measured D50 for abrupt spring temperature regimes ranged from 0.02 to 5.8 days and averaged 1.4 days. The model underestimated D50 for gradual spring temperatures for cane beardgrass (*Bothriochloa barbinodis* Herter), Arizona cottontop, and green sprangletop [*Leptochloa dubia* (H.B.K.) Nees] while overestimating D50 for all other grasses. The model underestimated D50 for abrupt spring temperatures for all the lovegrasses and overestimated D50 for the other grasses.

A linear regression model estimated 1/D50, and consequently D50, more accurately than the polynomial model for winter temperatures. The linear model of 1/D50 on constant temperature was constructed using only suboptimal and optimal temperatures and omitting supraoptimal temperatures (Table 4). Minimum estimated temperatures for germination from this linear model ranged from 7.1 to 11.3°C and averaged 8.1°C for the 12 collections tested. The linear model underestimated D50 of bush muhly by 25 to 30 days for gradual winter temperatures. Absolute differences between estimated and measured D50 for gradual winter temperatures for the other 10 collections averaged only 2.8 days. The model tended to slightly overestimate D50 for most native grasses and Cochise lovegrass and underestimate D50 for sideoats grama and the Lehmann lovegrass collections for this temperature regime. The linear model underestimated D50 of the bush muhly and Lehmann lovegrass collections by 17 and 11 days, respectively, for abrupt winter temperatures. The model underestimated D50 of the other collections by an average of 4.3 days for this temperature regime.

Table 3. Time to 50% germination (days) for 15 warm-season grasses under constant, gradual and abruptly alternating temperatures representative of wet seedbed conditions in a southeastern Arizona desert grassland.

Species	Summer			Winter			Spring		
	Constant[1]	Gradual	Abrupt[2]	Constant	Gradual	Abrupt	Constant	Gradual	Abrupt
	Time to 50% germination (days)								
Cane beardgrass	1.7abE[3]	1.4bC	2.3aA	1.5bE	12.6aDE	17.0aC-F	1.6bB	2.7aB	2.7aE-F
Sideoats grama	1.8abE	1.4bC	1.9aA	1.5bE	13.1aDE	12.8aF	1.6cB	3.3aB	2.4bF
Arizona cottontop	3.4aC-E	2.3bBC	3.1abA	2.2cC-E	17.5bC-E	26.7aA-E	2.8bB	4.9aB	4.3aC-F
Tanglehead	2.2aDE	1.6bC	1.6bA	1.6bDE	10.4aE	9.8aF	1.6cB	3.0aB	2.3bF
Green sprangletop	2.7bC-E	3.1bAB	3.8aA	2.1cC-E	12.5bDE	14.0aEF	2.6bB	5.6aB	5.8aB-D
Bush muhly									
Arizona	2.7abDE	2.3bBC	3.2aA	1.6bDE	>42	33.9aAB	1.7bB	6.6aAB	3.4bD-F
New Mexico	1.8abE	1.6bC	2.3aA	1.5cE	36.6aAB	19.4bB-F	1.2bB	4.7aB	2.7bE-F
Bristlegrass	6.3aBC	3.6bA	5.0abA	3.4bBC	24.9aB-D	37.1aA	6.1aAB	9.6aAB	10.0aA
Plains bristlegrass	16.6aA	–	14.0aA	6.0bA	26.9aBC	36.4aA	15.1aA	17.6aA	10.9aA
Plains lovegrass	3.4aB-D	2.3bBC	3.2aA	2.8bB-D	19.0aC-E	19.8aB-F	3.0cB	6.3aAB	5.7bB-D
Lehmann lovegrass									
2814	5.4aB	3.7bBC	2.1cA	3.8cB	24.2bB-D	27.4aA-E	4.3cAB	8.1aAB	5.9bBC
9178	6.0aB	3.2bAB	4.2bA	4.1bB	29.0aBC	30.9aA-D	4.0bAB	8.4aAB	7.4aB
9247	7.0aDE	2.2cBC	3.9bA	1.7bDE	26.2aBC	32.3aA-C	4.3bAB	8.3aAB	6.5abBC
Cochise lovegrass									
6308	2.6aDE	1.7bC	2.7aA	1.7bDE	12.9aDE	12.9aF	2.2bB	5.1aB	5.0aB-E
9366	2.7aDE	1.7bC	2.6aA	1.8bDE	11.4aE	15.3aD-F	2.0bB	5.1aB	4.7aC-F

[1]Constant temperature was 25°C.
[2]Abruptly alternating temperature regimes remained at the cooler temperature for 16 hours and at the warmer temperature for 8 hours. Summer temperatures were 20-40; winter 1-16; and spring 2-33°C.
[3]Means of time to 50% germination among temperature regimes within a season for each seed collection followed by the same lower case letter and among seed collections within a column followed by the same upper case letter are not significantly different ($p<0.05$) by the Tukey HSD test.

Discussion

Laboratory germination percentages under conditions of unlimited moisture were high for most of these warm-season grasses under a variety of temperatures. These results are consistent with previous studies (Wilson 1931, Little 1937, Bridges 1941, Frasier et al. 1985, Ellern and Tadmor 1966, Livingston 1992, Roundy et al. 1992c). For most of the grasses, the constant 25°C and abruptly alternating temperature regimes produced similar total germination percentages and germination rates to the gradually fluctuating temperature regimes characteristic of wet summer seedbeds. Warm-season grasses are typically planted in the southwestern U.S. in the summer prior to the onset of the summer rainy season. For most of these species, a constant 20 to 25°C or abruptly alternating germination test should be adequate to estimate bulk seeding rates of nondormant seeds. Exceptions include some collections of Lehmann lovegrass. Two collections in this study, 9178 and 9247, had lower total germination under gradual summer temperatures than under constant or abrupt temperature regimes (Tables 2 and 3). The 3 Lehmann lovegrass collections in this study also had much slower germination under constant 25°C than under gradual or abrupt summer temperatures.

Table 4. Coefficients of determination for linear (r^2) and third-order polynomial (R^2) regressions of constant temperature (°C) on germination rate (days to 50% germination) and total germination (%) for 12 warm-season grasses. Linear and polynomial regressions apply to suboptimal and suboptimal to supraoptimal constant temperatures for germination, respectively. SEE=standard error of estimate. All regressions were significant at $p<0.001$.

Species	Linear regression for germination rate				Polynomial regression			
			Temperature threshold (°C)		Germination rate		Germination (%)	
	r^2	SEE	Minimum	Maximum	R^2	SEE	R^2	SEE
Cane beardgrass	0.90	0.073	7.8	30	0.83	0.106	0.85	9.8
Sideoats grama	0.80	0.159	6.7	25	0.85	0.112	0.70	17.4
Arizona cottontop	0.53	0.130	9.9	35	0.53	0.142	0.61	7.3
Green sprangletop	0.67	0.143	8.6	35	0.83	0.105	0.82	13.8
Bush muhly								
Arizona	0.88	0.113	7.1	35	0.93	0.085	0.93	11.6
New Mexico	0.89	0.108	7.3	30	0.91	0.097	0.89	10.9
Plains lovegrass	0.95	0.052	7.4	35	0.92	0.067	0.93	10.6
Lehmann lovegrass								
2814	0.93	0.067	8.6	40	0.86	0.091	0.64	17.3
9178	0.83	0.085	9.5	40	0.79	0.094	0.48	12.8
9247	0.73	0.148	11.3	40	0.70	0.153	0.38	24.0
Cochise lovegrass								
6308	0.95	0.060	6.3	35	0.93	0.067	0.75	16.2
9366	0.96	0.055	6.7	35	0.91	0.082	0.80	12.6

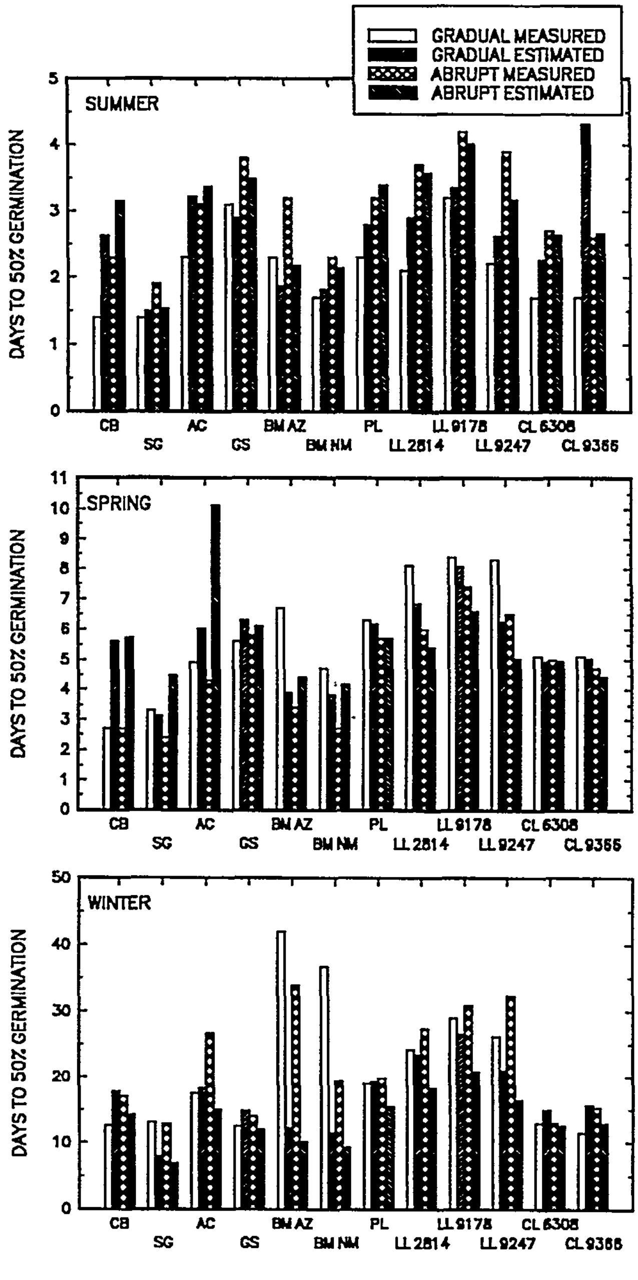

Fig. 3. Measured days to 50% germination for gradual and abruptly fluctuating temperature regimes compared to estimates from linear (winter) and third-order polynomial (summer and spring) regressions of germination rate (1/days to 50% germination) on constant temperature. Warm-season grasses were CB, cane beardgrass; SG, sideoats grama; AC, Arizona cottontop; GS, green sprangletop; BM AZ, NM, bush muhly collected in Arizona and New Mexico, respectively; PL, plains lovegrass; LL 2814, 9178, 9247, Lehmann lovegrass collections; CL 6308 and 9366, Cochise lovegrass collections.

Bristlegrass was the only species that did not germinate well in this study (Table 2). Toole (1940) encountered similar difficulties and was able to improve germination by prechilling and scarification with sulfuric acid to break the hard seed coat. Alternating temperatures were insufficient to break dormancy of these species in this study.

Optimum constant temperatures for maximum total germination ranged from 20 to 30°C for native grasses and from 15 to 20°C for introduced lovegrasses (Fig. 2). However, optimum constant temperatures for germination rate, expressed as 1/D50, were 5 to 10°C higher for native grasses and 15 to 20°C higher for introduced lovegrasses (Fig.2, Table 4). For these species, most seeds germinate at cooler temperatures, but the fastest germinating seeds germinated at higher temperatures. Higher optimum temperatures for germination rate than for total percent germination is typical for many species (Roberts 1988).

Most of these species exhibited a typical response of total germination and germination rate to constant temperature; increasing to an optimum temperature, then decreasing quickly with supraoptimal temperatures (Roberts 1988). One exception was sideoats grama which maintained high total and rate of germination between 20 and 45°C temperatures (Fig. 2). This adaptation to a wide range of temperatures may, in part, contribute to the wide ecological amplitude of this species from warm desert grasslands to cooler northern plains grasslands. The classical and predictable germination responses of these species to constant temperatures permitted reasonable estimates of D50 for most of the species tested for diurnally dynamic, seasonal temperature regimes characteristic of the southwest desert grassland.

When model estimates of D50 are similar to measured D50 for both gradual and abrupt temperature regimes, cumulative temperature effects are indicated. This was the case for most of the collections. Differences between estimated and measured D50 could be associated with lack of precision in the model for some collections which can limit accuracy of specific estimates. Such differences could also be associated with germination responses which vary with seed age. This may be the case with Arizona cottontop which evidently was beginning to lose viability and had lower germination when constant temperature experiments were conducted.

Deviations between model-estimated and measured D50 could also indicate other physiological responses to temperature variability. Temperature extremes, cycles, and the rate of temperature change may induce or break dormancy of some seeds and alter the time required for seeds to germinate. Overestimation of D50 for gradual, and underestimation of D50 for abrupt summer temperatures, respectively, suggests that the summer gradual temperature curve had a stimulating effect on germination rate in addition to cumulative temperature effects (Fig. 3). Underestimation of D50 for the Lehmann lovegrass and bush muhly collections for both gradual and abrupt winter temperatures indicates sensitivity to cool temperature extremes for these species.

Model overestimation of D50 for the Lehmann lovegrass collections under gradual and abruptly alternating spring temperatures indicates that germination may be stimulated by extreme temperature alternations. Roundy et al. (1992c) found that collections of Lehmann lovegrass had higher germination when prechilled, or incubated at cool minimum temperatures (0 and 2°C for 16 hours) abruptly alternating with 20 and 30°C maximum temperatures (8 hours), than under warmer minimum temperatures. Low temperatures are effective in breaking dormancy of many species which then germinate at higher temperatures (Bewley and Black 1982). Roundy et al. (1992c) suggested that the relatively long warm period of abrupt laboratory temperature alternations may allow germination to proceed while the low cold period temperature helped to break dormancy for the lovegrasses they studied. For 2 of the lovegrass collections in the current study, an abruptly alternating spring temperature regime produced higher total germination than did a constant 25°C or a gradual temperature alternation (Table 2). Abrupt alternating temperatures may have broken dormancy for some seeds of these collections.

Total germination percentages of most of these warm-season grasses were high enough for field germination in summer, spring, or winter in the southwest desert grassland. Seedling establishment for these species is usually observed after summer rainfall. Emergence of many of these species in the winter is unlikely because surface soil water would have to be available for 2 to 3 weeks to achieve 50% germination. Similarly, soil moisture would have to be available for about a week to allow germination of some of these species under spring temperatures. High germination percentages and rates of the native grasses make them good candidates for rangeland revegetation and restoration projects under conditions of adequate soil moisture. Hourly field seedbed temperature averages could be used to estimate D50 and model seed germination when water is available for most of these species.

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