Temperature responses and calculated heat units for germination of several range grasses and shrubs

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Abstract

Quantitative effects of temperature on germination were determined for 17 cool-season grasses, 19 warm-season grasses, and 18 miscellaneous forbs and shrubs associated with semiarid rangelands. These effects, expressed as the reciprocal of days to 50% germination, were used in linear regression analyses to predict the temperature at which the germination rate approaches zero from which heat units to 50% germination and germination indexes were derived. The regression relationships appeared to be linear if data were restricted to the lower range of germination temperatures. The germination rate approached zero at temperatures ranging from 3.7 to 6.3° C for cool-season and from 7.8 to 13.7° C for warm-season grasses. No particular trend was evident among the forbs and shrubs. The reciprocal of the slope of the regression equation was a constant expressing heat units to 50% germination. It was characteristic of each accession. The product of heat units and the zero rate temperature was used to calculate a germination index. This index compared well with selected germination responses observed in the field.

Key Words: germination rates, base temperature, germination indices, semiarid rangelands

Germination, a critical stage in establishment of seedlings on semiarid rangelands, is often limited by temperature even when moisture conditions are favorable. Quantitative temperature effects on germination may be useful to evaluate germination characteristics or establishment potential among range species. Derived variables such as heat units to 50% germination, temperatures coinciding with minimum germination rates, and products of the 2 germination indices should be helpful for explaining variations in seedling establishment observed in field plantings.

The heat unit concept relates a unique total of periodic temperatures summed above a minimum temperature. This is then related to a specific growth stage (Wang 1960), provided no other factors are limiting growth (Kish and Ogle 1980). Arnold (1959) stated the most critical factor in using heat units was the accurate determination of the minimum or base temperatures, and he discussed the use of linear regression equations for their prediction. He further indicated that the purpose of these minimum temperatures was to develop heat units, an expression of effective temperature, usually on a daily basis.

Schimpf et al. (1977) indicated germination rates are a more sensitive indicator of temperature effects on germination than are total germination percentages. Maguire (1962) and Czabator (1962) stated that species having similar total germination percentages may vary widely in rate of germination and consequent seeding value. Jordan (1983) illustrated that within a seed lot, establishment typically occurs on semiarid sites from seeds having the earliest germination. Methods used to express germination rates vary widely (Kotowski 1926, Czabator 1962, Tucker and Wright 1965, Evetts and Burnside 1972). Therefore, published rates among species are not always related and easily compared. However, the germination rate index of Evetts and Burnside (1972), Pollack and Roos (1972), and the corrected germination rate of Hsu et al. (1985) are equivalent. Moreover, the data of Hsu et al. (1985) showed that dividing 100 by their corrected germination rate gave an approximation of time to 50% germination. Hegarty (1975) and Garcia-Huidobro et al. (1982a) showed a linear relationship between the reciprocal of time to 50% germination and certain optimum or lower germination temperatures. Angus et al. (1981) and Hsu et al. (1985) indicated this relationship was not linear, but it still gave the best estimate of the temperatures corresponding with minimum germination rate used to develop heat units and to characterize germination (Garcia-Huidobro et al. 1982a, Davidson and Campbell 1983).

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It appears that quantitative temperature effects can be determined to characterize temperature-responsive germination rates. This paper reports on the determination of projected minimum temperatures, heat units, and germination rates for several rangeland species.

Materials and Methods

Seeds were obtained from commercial sources, from USDA Soil Conservation Service, Tucson Plant Materials Center, and from range sites identified by county and state. All seed lots were hand thrashed when necessary and further processed by air flotation to remove trash and poorly filled seeds.

Germination was conducted at constant temperatures in a germinator having forced-draft circulation. Light was not controlled, but was allowed to enter through the glass doors of the germinator. Three series of studies were conducted: cool-season grasses with 4 replications, warm-season grasses with 3 replications, and selected forbs and shrubs with 4 replications. Germination temperatures were 7, 14, and 21° C for cool-season grasses; 15, 20, and 30° C for warm-season grasses; and 5, 10, 20, and 30° C for forbs and shrubs. Replications for each species were completely randomized within the germinator for each temperature. For each replication 100 seeds were sprinkled into a 9-cm petri dish on Whatman[1] No. 3 filter paper moistened with tap water.

Rapidly germinating seeds were observed for germination every 6 hours during the first week after imbibition began. Otherwise, seeds were observed every 12 hours for the first week, every day for the second week, and every 2 days thereafter up to a total of 60 days at low temperatures. Germinated seeds were counted, recorded, discarded, and water added when necessary. Seeds were considered germinated when the radicle was at least 1-mm long. Germination was considered complete when no further germination occurred in 2 successive days.

Starting from the time imbibition began, the number of seeds germinated at each count was tabulated with the corresponding accumulated time. After each germination trial was completed,

[1]Mention of a trademark or proprietary product does not constitute a guarantee or warranty of the product by U.S. Department of Agriculture or the University of Arizona and does not imply approval to the exclusion of other products that may also be suitable.

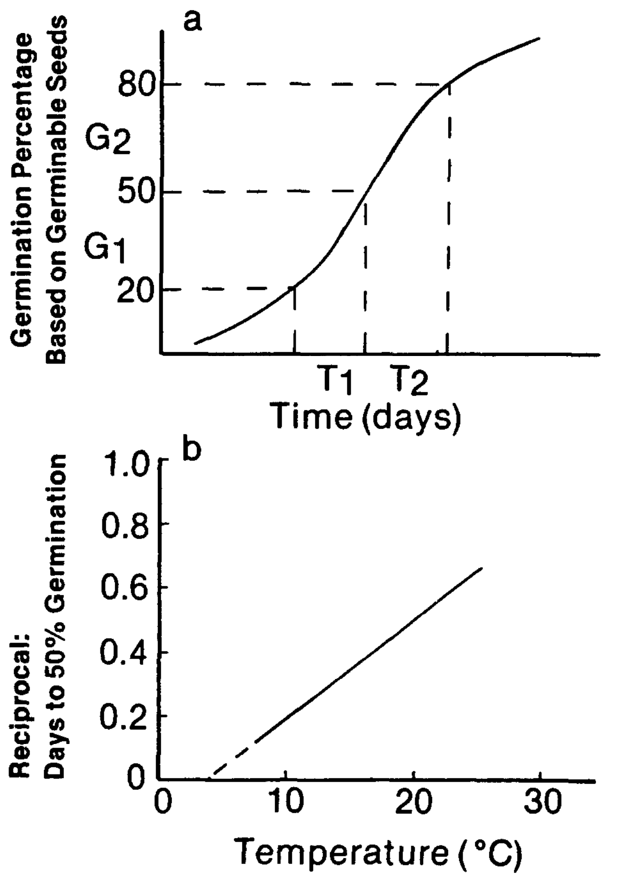

Fig. 1. *(a) The linear portion of the S-shaped function of the germination curve used in equation (1) and (b) illustration of regression analysis and extrapolation used to determine temperature at which germination rate approached zero.*

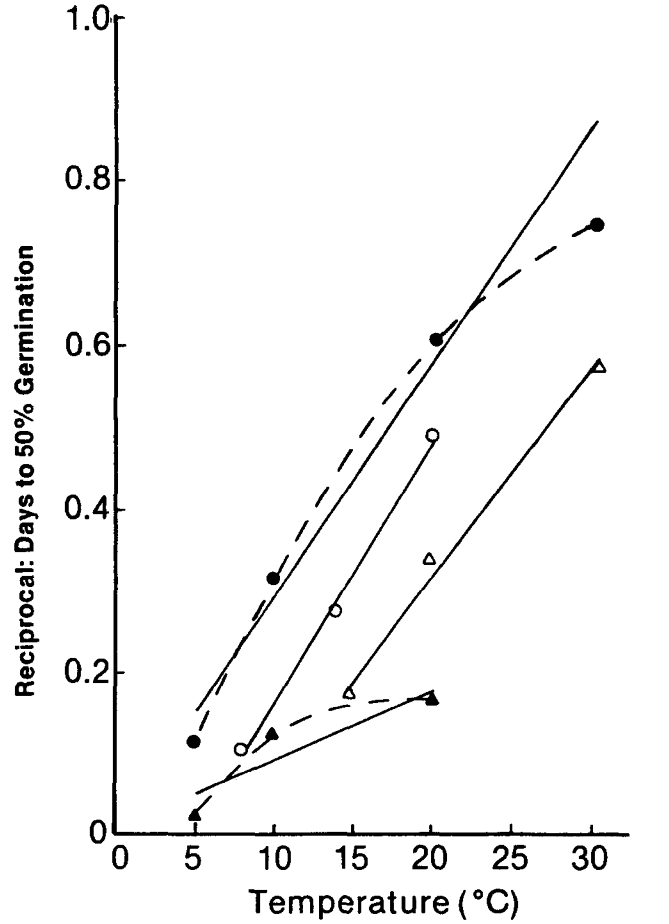

Fig. 2. *The relationship of germination to temperatures for* •, Atriplex canescens; o, Bromus inermis; Δ, Panicum antidotale; *and* ▲, Ephedra viridis. *Solid lines fitted from linear regression equations; dashed lines follow actual data where inhibitory high temperatures affected* • *and* ▲.

total percent germination was determined and each count was converted to percent germinable seed. Rate determinations were based on the equivalence of 100 germinable seeds for each accession. Time to 50% germination was calculated by equation (1) which restricts calculations to the linear portion of the S-shaped function of the germination curve (Fig. 1a).

$$\text{Time to 50\% germination} = T_1 + \frac{50 + G_1}{G_2 - G_1} \; T_2 - T_1 \qquad [1]$$

where G_1 = cumulative % germination between 20 and 50% at T_1
and G_2 = cumulative % germination between 50 and 80% at T_2

Regression analyses, both linear and quadratic, were conducted on each ecotype or species using the reciprocal of time to 50% germination as the dependent (y) variable and temperature as the independent (x) variable (Fig. 1b). If the quadratic function was significant, graphs were constructed and inspected to determine if some portion of the curve was sufficiently linear for further use (Fig. 2). Analyses of variance were also conducted on the linear and quadratic functions to determine which expressed the best relationship between temperatures and germination rates within species. When both linear and quadratic functions were significant (P = 0.05 to 0.01), the percentage of total sums of squares contributing to each function was determined to further clarify this relationship (Snedecor 1956). Linear relationships are important for calculating the projected minimum temperature at which the germination rate is equal to zero. The minimum temperature was estimated by setting y = 0 in the linear regression equation and solving for x (Fig. 1b). Heat units/day, a measure of effective daily temperature (Arnold 1959), was calculated by equation (2).

$$\text{Heats units/day} = \text{Mean daily temperature} - \text{Minimum temperature} \qquad [2]$$

A heat unit index was calculated by equation (3).

$$\text{Heat unit index} = (\text{Heat units/day}) \times (\text{Days to 50\% germination}) \qquad [3]$$

The heat unit index is a constant for each species within favorable temperatures above the zero germination rate. It expresses heat units required to attain 50% germination, the reciprocal of which is used to determine the slope of the linear regression equation.

Results and Discussion

Coefficients of linear regression and levels of significance of the linear and quadratic regression analyses are presented in Table 1 for cool-season grasses, in Table 2 for warm-season grasses, and in Table 3 for forbs and shrubs. The linear component of regression was highly significant (p = 0.01) for all species. The quadratic component was generally not significant for various cultivars of grasses, but was generally highly significant (p = 0.01) for shrub ecotypes.

Even though Figure 2 illustrates a "worst case scenario", for certain species having a highly significant (p = 0.01) quadratic function (Tables 1, 2 and 3), visual inspection indicated linearity

Table 1. Linear coefficients of determination, quadratic regression significance, minimum germination rate temperatures, heat units to 50% germination and germination indices for selected cool-season range grasses. Linear regressions were of the form y = a + bx where y = 1/days to 50% germination, a = intercept, b = slope, and x = temperature.

Species	r^2	Quadratic significance level	% ss[1]	Min. temp.	Heat units	Germ. indices
Agropyron elongatum 'Largo'	0.995	n.s.		4.3	30.2	130
Agropyron elongatum 'Jose'	0.980	n.s.		4.7	30.5	143
Bromus inermis 'Lincoln'	0.985	0.01	0.8	4.9	31.0	152
Elymus cinereus 'Coconio Co. Az.	0.984	n.s.		5.3	29.6	157
Agropyron tricophorum 'Luna'	0.983	0.05	0.9	5.5	29.6	163
Agropyron intermedium 'Tegmar'	0.954	n.s.		4.4	37.4	164
Agropyron intermedium 'Greenar'	0.943	n.s.		5.0	33.2	166
Agropyron dasystachyum 'Critana'	0.958	n.s		4.5	41.3	186
Agropyron riparium 'Sodar'	0.997	0.01	1.6	4.5	46.5	209
Agropyron inerme 'Whitmar'	0.878	0.01	7.5	6.3	42.7	269
Poa ampla 'Sherman'	0.989	n.s.		3.7	72.9	269
Agropyron desertorum 'Nordan'	0.971	n.s.		4.8	60.9	292
Agropyron cristatum 'Fairway'	0.943	n.s.		5.0	62.9	314
Elymus junceus 'Vinall'	0.970	n.s.		5.8	58.6	340
Agropyron smithii commercial	0.955	n.s.		4.5	85.5	384
Oryzopsis hymenoides commercial	0.848	n.s.		4.7	87.5	411
Elymus junceus commercial	0.960	n.s.		5.0	90.6	453

[1]Percentage sum of squares attributed to quadratic component of regression $P = 0.05$ to 0.01.

was not strongly affected until over 5 to 10% of the regression sum of squares was contributed by the quadratic function. The quadratic contribution was 0.8% for *Bromus inermis*, 7.0% for *Atriplex canescens*, 9.0% for *Panicum antidotale*, and 19.0% for *Ephedra viridis*. Linearity was deemed acceptable for the *Bromus* and *Panicum* selections, but not acceptable for *Atriplex* accessions because of obvious inhibition of rates above 20° C. For *Ephedra*, linearity up to 20° C was not acceptable. Thus, rates for the latter 2 species, reported here for purposes of illustration, should be recalculated from germination studies conducted at a lower temperature range.

Aside from the few exceptions illustrated in Figure 2, relationships between the reciprocal of time to 50% germination and germination temperature were sufficiently linear over a wide array of species and ecotypes to allow calculation of projected times to 50% germination and temperatures associated with minimum germination rates. When heat units are included, the general requirements for germination of an accession can be characterized as for *Poa ampla* var. Sherman at 10° C (Table 1). The minimum temperature 3.7° C is subtracted from 10.0° C to obtain heat units/day, i.e., 6.3. When heat units to 50% germination (reciprocal of the slope b) are divided by heat units/day the quotient is equal to days to 50% germination at 10.0° C (72.9/6.3 = 11.5 days). Alternatively, regression coefficients –0.0507(a) and 0.0137(b) can be used to solve for y, the reciprocal of time to 50% germination

Table 2. Linear coefficients of determination, quadratic regression significance, minimum germination rate temperatures, heat units to 50% germination and germination indices for selected warm-season range grasses. Linear regressions were of the form y = a + bx where y = 1/days to 50% germination, a = intercept, b = slope, and x = temperature.

Species	r^2	Quadratic significance level	% ss[1]	Min. temp.	Heat units	Germ. indices
Cenchrus ciliaris P-15625[2]	0.999	n.s.		12.5	5.9	74
Pennisetum setaceum commercial	0.999	n.s.		11.0	6.7	74
Bouteloua curtipendula NM-28	0.993	0.05	0.5	8.9	8.5	76
Bouteloua eriopoda 'Sonora'	0.992	0.01	0.5	13.0	5.9	77
Leptochloa dubia A-14254	0.964	0.05	3.0	13.0	6.9	90
Setaria macrostachya commercial	0.879	0.01	11.8	11.1	8.3	92
Bothriochloa ischaemum P-15626	0.996	n.s.		13.7	7.4	101
Bouteloua gracilis 'Hachita'	0.975	n.s.		10.6	10.0	106
Eragrostis lehmanniana × *E. tricophora*, 'Cochise'	0.998	n.s.		10.2	10.6	108
Eragrostis intermedia A-19189	0.938	n.s.		8.8	15.5	136
Eragrostis lehmanniana A-68 (lot 6101)	0.994	n.s.		10.8	12.8	138
Digitaria californica A-16154	0.987	0.01	1.0	13.5	11.6	157
Eragrostis curvula var. *conferta*, 'Catalina'	0.998	n.s.		10.8	14.8	160
Eragrostis lehmanniana A-68 (lot 6092)	0.937	n.s.		13.4	12.4	166
Sporobolus airoides NM-184	0.999	n.s.		12.0	16.0	192
Eragrostis lehmanniana L-19	0.993	n.s.		12.4	16.9	210
Panicum coloratum commercial	0.993	n.s.		9.7	29.5	286
Panicum antidotale A-130	0.989	0.01	9.1	7.8	38.3	299
Eragrostis curvula var. *conferta*, A-84	0.998	n.s.		11.2	39.7	445

[1]Percentage sum of squares attributed to quadratic component of regression, $P = 0.05$ to 0.01.

[2]Numbers are accession numbers assigned by USDA, SCS, Plant Materials Center.

(Table 1). Quantitative evaluations of temperature have shown that 11.5 days at 10° C are required for germination of this species, but emergence would obviously require additional time. It is recognized, however, that these germination values are relative because field and laboratory responses will probably differ from one another.

Inhibition of germination rates by comparatively high temperature is considered to be the major cause of non-linearity in our study (Arnold 1959). When a highly significant quadratic component ($p = 0.01$) was present (Tables 1, 2, 3), higher germination temperatures demonstrated a higher requirement for heat units/day than predicted by the use of the linear regression equation (Arnold 1959, Garcia-Huidobro et al. 1982a). Angus et al. (1981) used a similar heat unit study to estimate time to emergence for various field crops. They obtained non-linear relationships for some crops, but they could not improve on their estimates by non-linear models. Hsu et al. (1984) indicated that minimum germination temperatures, as used for determining germination rates in our study, were best estimated from linear regression analyses.

Table 3. Linear coefficients of determination, quadratic regression significance, minimum germination rate temperatures, heat units to 50% germination and germination indices for selected forbs and shrubs. Linear regressions were of the form y = a + bx where y = 1/days to 50% germination, a = intercept, b = slope, and x = temperature.

Species	r^2	Quadratic significance level	% ss[1]	Min. temp.	Heat units	Germ. indices
Ceratoides lanata Cochise Co., Az.	0.882	0.01	10.7	0.5	11.9	6
Ceratoides lanata Cochise Co., Az.	0.970	0.01	10.7	1.2	17.3	21
Baccharis sarothroides Pima Co., Az.	0.983	0.01	1.0	3.5	14.3	50
Atriplex canescens Millard Co., Utah	0.885	0.01	7.1	1.5	38.5	58
Ceratoides lanata Garfield Co., Utah	0.938	n.s.		3.3	18.7	62
Mimosa biuncifera Gila Co., Az.	0.784	n.s.		1.4	71.5	100
Cowania stansburiana Coconino Co., Az.	0.985	0.05	0.5	1.5	85.1	128
Atriplex canescens Rio Arriba Co., N.M.	0.843	0.01	9.7	2.6	55.2	144
Ephedra viridis Sevier Co., Utah	0.764	0.01	19.0	1.2	119.9	144
Atriplex semibaccata 'Corto'	0.924	0.01	5.4	1.8	86.2	155
Prosopsis juliflora Pima Co., Az.	0.948	0.01	4.0	10.3	17.4	179
Cowania stansburiana Yavapai Co., Az.	0.987	0.01	0.9	1.1	172.2	182
Fallugia paradoxa Yavapai Co., Az.	0.989	0.01	0.8	4.4	46.0	207
Acacia greggii Pinal Co., Az.	0.985	n.s.		7.2	29.3	211
Larrea tridentata Greenlee Co., Az.	0.950	0.01	4.0	6.8	40.6	276
Atriplex canescens Pima Co., Az.	0.984	n.s.		9.0	34.9	314
Ephedra viridis Sanpete Co., Utah	0.773	0.01	8.6	2.2	201.0	442
Linum lewisii 'Appar'	0.828	0.01	15.0	3.2	174.3	558

[1]Percentage sum of squares attributed to quadratic component of regression $P = 0.05$ to 0.01.

This approach proved valid even though some non-linearity was evident.

Application of Projected Minimum Temperatures

The projected minimum temperature is where the germination rate equals zero. Whether or not this projected temperature coincides with the physiological minimum temperature does not detract from the thesis that heat units can be used to characterize germination. The primary function of using base temperatures is to give the least variation among heat unit summations (Arnold 1959). Generally prediction of minimum temperatures and heat units will be more accurate when obtained from lower temperature ranges. Our studies also confirmed this trend. Moreover, when the minimum germination temperature was closely approached, time to accomplish germination increased. This may be critical in the field, particularly if germination time greatly exceeds the time that soil moisture is normally available. Data for *P. ampla* illustrates the principle. If the mean germination temperature was changed to 5° C, the time to 50% germination would be 56 days, and at 4° C it would be 243 days. Projection of values beyond data used to establish the linear regression is obviously not valid. However, the general trend for long germination periods as minimum temperatures are approached is clearly established.

The apparent variation in minimum germination temperatures as reported in the literature is often due to differences in methodology or research objectives. Young and Evans (1982), for example, reported germination percentages of several cool-season grasses at lower temperatures than we measured (Table 1). Similarly, Coffman (1923) found wheat *(Triticum aestivum)* and other small grains would germinate at the temperature of melting ice. These endpoint temperatures differ from those determined as the germination rate equals zero. The germination rate of wheat approaches zero at 4.6° C (Davidson and Campbell 1983). Hsu et al. (1985) and Garcia-Huidobro et al. (1982a) reported temperatures associated with minimum germination rates for warm-season grasses that were within the range that we found (Table 2).

A marked trend occurred within plant classifications. Minimum temperatures were lower for cool- (Table 1) than for warm-season species (Table 2). Values ranged from 3.7 to 7.8° C for cool-season and from 7.8 to 13.7° C for warm-season species. This trend was not associated with the shrubs (Table 3). The species *Larrea tridentata* and *Mimosa biuncifera* had minimum temperatures of 6.8 and 1.4° C, respectively. Both are warm-season shrubs. Moreoever, minimum temperatures for ecotypes of *Atriplex canescens* were 1.5, 2.6, and 9.0° C (Table 3), depending on location of seed collection sites. In contrast to the more uniform characteristics of released varieties, a wide variation in minimum temperatures may exist for wildland ecotypes.

Further research is needed to integrate the various factors affecting germination rates. Several examples of variations in temperature reponse are reported in the literature. Cluff et al. (1983) demonstrated that *Distichlis spicata* var. *stricta* would not germinate unless exposed to at least a 20° C diurnal temperature fluctuation. Young and Evans (1982), however, found maximum germination percentages could be obtained in constant temperatures for most of the cool-season grasses they studied. Finally, germination percentages and rates may vary among seed lots as well as plant ecotypes (Weaver and Jordan 1985).

Heat Units and Germination Indexes

Arnold (1959) defined the heat unit as a biologically effective temperature. Therefore, heat units are accumulated only during temperatures above a minimum (Holmes and Robertson 1958) and below a maximum that allow for growth processes of the target species (Garcia-Huidobro et al. 1982b). During a 10-year period, successful seedling emergence was observed from fall seeding on *Artemisia tridentata* sites only when mean monthly temperatures during the fall, winter and spring were above 0° C, and 76 to 102 mm of effective precipitation occurred over the winter (Jordan 1983). Some species and cultivars consistently established more dependably than others. For example, in order of increasing establishment difficulty were *Agropyron tricophorum* var. Luna, *A. desertorum* var. Nordan, *Elymus junceus* var. Vinall, *Oryzopsis hymenoides* and *E. junceus* common. The trend for ease of establishment (Jordan 1981) was associated with low values of heat units required to attain 50% germination (Table 1). In addition, Arnold (1959) indicated the lower the minimum germination temperature the higher the germination efficiency. The cumulative effect of low heat unit values and low minimum temperature can be expressed as a germination index, equation (4).

$$\text{Germination index} = (\text{Heat unit index}) \times (\text{Minimum germination rate temperature}) \quad [4]$$

For these 5 species, the respective heat unit indices were 163, 292, 340, 411, and 453.

Without knowledge of seedling drought tolerance, germination indices may not be as helpful for warm- as for cool-season grasses. Low indices, indicating high germination rates, may be a disadvantage on semiarid sites for establishment of selected species without high seedling drought tolerance. For example, *P. antidotale* and *Eragrostis lehmanniana* × *E. tricophora* var. Cochise have been established on sites too arid for *Bouteloua curtipendula* (Jordan 1981), but their respective indexes were 299, 108, and 76. Frasier et al. (1984) and Simanton and Jordan (1986) showed *B. curtipendula* seeds germinated rapidly. However, Frasier et al. (1984) found a high percentage of seedlings succumbed during the following dry period, whereas Cochise seeds germinated more slowly but had fewer dying during the dry period. These examples suggest seedling drought tolerance may be a necessary complement to high germination rates for successful establishment of selected grass species on rangelands where the amounts and timing of precipitation are sporadic.

In summary, heat units, germination indices, and germination rates can provide selection criteria among accessions within semiarid environments. These factors can be derived through regression analyses provided that the temperature range is restricted to an estimated 15 to 20° C above the temperature associated with the minimum germination rate. Observations made during this study indicate to obtain uniformity in reporting germination rates in the literature requires that germination temperatures must be determined accurately, equivalent end points of germination rates must be presented, and rates must be expressed only on basis of germinable seed.

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