

Variability in Thermal Response of Primed and Non-primed Seeds of Squirreltail [*Elymus elymoides* (Raf.) Swezey and *Elymus multisetus* (J. G. Smith) M. E. Jones]

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Received: 5 October 2001 Returned for revision: 12 November 2001 Accepted: 26 November 2001

Bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey = *Sitanion hystrix* (Nutt.) J. G. Smith] and big squirreltail [*Elymus multisetus* (J. G. Smith) M. E. Jones = *Sitanion jubatum* (J. G. Smith)] have a broad geographical distribution and have been identified as high priority species for restoration of degraded rangelands in the western United States. These rangelands exhibit high annual and seasonal variability in seedbed microclimate. The objective of this study was to examine variability in thermal response of both primed and non-primed seeds of these species in the context of field-variable temperature regimes. Seed priming treatments were selected to optimize germination rate in a low-temperature test environment. Primed and non-primed seeds were evaluated for laboratory germination response under 12 constant temperature treatments between 3 and 36 °C. Thermal time and base temperature were estimated by regression analysis of germination rate as a function of temperature in the sub-optimal temperature range. The thermal germination model and 6 years of field temperature data were used to simulate the potential germination response under different field planting scenarios. Seed priming reduced the total germination percentage of some seedlots, especially at higher germination temperatures. Seed priming increased the germination rate (reduced the number of days to 50 % germination) by 3.8–8.4 d at 6 °C with a mean germination advancement of 6.9 ± 0.6 d. Maximum germination advancement in the model simulations was 5–10 d for planting dates between 1 March and 15 May. Model simulations can be used to expand germination analysis beyond simple treatment comparisons, to include a probabilistic description of potential germination response under historical or potential future conditions of seedbed microclimate.

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Key words: Germination, priming, temperature, *Elymus elymoides* (Raf.) Swezey, *Elymus multisetus* (J. G. Smith) M. E. Jones, squirreltail, model.

INTRODUCTION

Critical factors determining establishment success in rangeland seedlings are the spatial and temporal distribution of soil heat and moisture relative to the growth response of desirable plants and their weedy competitors (Roundy and Call, 1988). Seedbed heat and moisture relationships are determined by the interaction of soils, vegetation and atmospheric parameters, which are highly variability over space and time (Call and Roundy, 1991; Pierson and Wight, 1991; Pierson *et al.*, 1992). Thermal and hydrothermal response models can be used to assess the effect of environmental variability on seed germination and seedling establishment (Garcia-Huidobro *et al.*, 1982a, b; Gummerson, 1986). Such models have been developed for some rangeland species (Jordan and Haferkamp, 1989; Romo and Eddleman, 1995; Meyer *et al.*, 2000) but relatively few have been used to evaluate the potential field response under various seedbed microclimates (Roundy and Biedenbender, 1996; Hardegree and Van Vactor, 1999, 2000).

Bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey = *Sitanion hystrix* (Nutt.) J. G. Smith] and big squirreltail [*Elymus multisetus* (J. G. Smith) M. E. Jones = *Sitanion jubatum* (J. G. Smith)] have a broad geographical distribution in the western United States and are adapted to a wide range of environmental conditions (Clary, 1975). These early to mid-seral, native perennial grasses have been identified by the Bureau of Land Management as high priority plant materials for restoration of degraded rangelands in the intermountain region of the western United States. Millions of acres of these rangelands have been invaded by exotic annual weeds such as cheatgrass (*Bromus tectorum* L.) and medusahead wild rye (*Taeniatherum caput-medusae* [L.] Nevski) (Young and Longland, 1996; Jones, 1998; Clausnitzer *et al.*, 1999). These weed species germinate rapidly at low temperatures and compete aggressively for soil and water resources early in the spring growing season (Young *et al.*, 1987; Young, 1992). Young and Evans (1977) investigated the germination response of bottlebrush squirreltail and found that its seeds germinate under a wide range of thermal conditions. Their study did not evaluate intraspecific variability in germination response and did not include specific information regarding germination rate.

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TABLE 1. Water potential at priming for 11 seedlots of squirreltail

Species	var.	Accession number	Collection site	Optimized priming water potential (MPa)
<i>E. elymoides</i>	<i>elymoides</i>	1108	Butte Co., ID	-1.0
<i>E. elymoides</i>	<i>elymoides</i>	1112	Butte Co., ID	-1.3
<i>E. elymoides</i>	<i>elymoides</i>	1116	Custer Co., ID	-1.3
<i>E. elymoides</i>	<i>elymoides</i>	1117	Custer Co., ID	-1.6
<i>E. elymoides</i>	<i>elymoides</i>	1127	Jefferson Co., MT	-1.0
<i>E. elymoides</i>	<i>californicus</i>	1104	Elko Co., NV	-1.3
<i>E. elymoides</i>	<i>brevifolius</i>	1105	Huerfano Co., CO	-1.6
<i>E. elymoides</i>	<i>brevifolius</i>	1122	Rio Blanco Co., CO	-1.3
<i>E. multisetus</i>		1103	Douglas Co., NV	-1.9
<i>E. multisetus</i>		1106	Whitman Co., WA	-1.6
<i>E. multisetus</i>		1136	Lassen Co., CA	-1.9

Seeds were primed for 6 d at 20 °C and then dried for 7 d before evaluation.

Hardegree (1994a, b, 1996), Hardegree and Van Vactor (2000) and Meyer *et al.* (2000) have demonstrated that seed priming treatments can be used to improve the thermal germination response of native perennial grass species in both the laboratory and the field. These authors have also investigated thermal and hydrothermal germination responses of both primed and non-primed bottlebrush squirreltail seeds, but only for a limited number of seedlots. The objectives of this study were to examine variability in thermal germination response of primed and non-primed squirreltail seeds, and to assess the potential for low-temperature germination enhancement under alternative field temperature scenarios.

MATERIALS AND METHODS

Seeds of squirreltail populations originating from field sites in California, Montana, Washington, Nevada, Colorado and Idaho were produced in a common environment at Greenville Farm (North Logan, UT, USA) in 1995 (Table 1). Seeds were threshed, cleaned and stored in paper envelopes at 4 °C until required for experimental purposes (1998).

Priming optimization

Optimal priming conditions of water potential and treatment duration were determined according to the procedure suggested by Hardegree (1996). Four replicate samples of 30 seeds from each seedlot were primed at -0.4, -0.7, -1.0, -1.3, -1.6, -1.9 and -2.2 MPa for either 4, 6 or 8 d in a controlled-temperature room at 20 °C. Water potential control during priming was maintained by placing seeds on top of cellulose membranes, in contact with a solution reservoir of polyethylene glycol 8000 (PEG) (Hardegree and Emmerich, 1992a). Initiation of priming was staggered so that all treatments ended on the same day. Each replicate sample was randomized within each of four blocks in the controlled-temperature room. After priming, seeds were removed from the treatment vials and dried on the laboratory bench at 20 °C for 7 d (Hardegree, 1994b). Water potential/duration combinations that resulted in >3 %

germination during priming were excluded as potential priming treatments.

Primed seeds from each test treatment were germinated at 10 °C to determine the optimal combination of priming water potential and treatment duration for each seedlot. Primed/dried seeds were germinated in programmable environmental chambers of the type described by Hardegree and Burgess (1995). A computer monitoring and control system evaluated chamber temperature every 3 min and adjusted the temperature whenever the measured temperature deviated from the programmed temperature by ≥ 0.5 °C. A datalogger monitored chamber temperature every 10 s and recorded an average temperature value for every 15 min period. Chamber lights, which maintained a photon irradiance of 16.0 ± 0.4 W m⁻², were activated for 12 h d⁻¹ starting at 0600 h.

Primed seeds were germinated in the same matric-potential control system used for priming (Hardegree and Emmerich, 1992a). However, the osmotic solution in the germination vials was mixed to a water potential of -0.03 MPa (Michel and Radcliffe, 1995). This water potential eliminated free solution on top of the membrane but was insufficient to induce significant water stress. Seeds were monitored daily for 21 d and seeds counted and removed when radicle extension ≥ 2 mm was observed.

Optimal priming conditions were determined by inspection of relative germination rate from the cumulative germination curves at 10 °C as a function of priming water potential and treatment duration. A 6 d treatment interval was selected as the best treatment duration across all seedlots. Optimal water potentials for priming with a 6 d treatment duration were between -1.0 and -1.9 MPa depending on the seedlot (Table 1).

Thermal evaluation of primed seeds

Seeds were primed for 6 d at the optimal water potential for priming and then dried on the laboratory bench for 1 week before the germination experiment (Hardegree, 1994b). A germination test was conducted on both primed and non-primed seeds at 12 constant temperatures between 3 and 36 °C. Germination vials for each treatment were replicated twice within each chamber and each temperature

regime was replicated simultaneously in three separate chambers. Germination vials containing 30 seeds were monitored every day for 28 d and the seeds were counted and removed when they exhibited radicle extension of ≥ 2 mm. Seeds were dusted with Daconil fungicide wettable powder (2,4,5,6-tetrachloro-1,3-benzenedicarbonitrile) at the beginning of a given experimental run and as needed thereafter to minimize fungal growth.

Germination counts were pooled by seedlot and priming treatment within each chamber and the within-box totals were considered replicate samples for model development and analysis. Two germination indices were calculated for each treatment replicate: total percentage germination; and time required to reach 50 % germination (d) based on the total number of seeds. Time required to achieve 50 % germination was calculated by interpolation from the cumulative germination curve (Covell *et al.*, 1986). Germination rate was considered to equal the inverse of the number of days required to reach 50 % germination (Arnold, 1959). A linear regression equation was derived to relate germination rate to temperature in the sub-optimal temperature range (Hardegee *et al.*, 1999). Thermal time (θ , °d) was estimated as the inverse slope of the regression line, and base temperature (T_b) was calculated by extrapolation to the point where the germination rate was zero.

Model simulation of field-temperature response

Predicted germination response to field-temperature regimes was simulated with soil data measured at the Orchard Field Test Site in south-eastern Ada County, Idaho, USA. These data represent the average of thermocouple temperatures measured every hour, between 1 March and 15 June, at a depth of 1 cm, in a Tindahay sandy-loam soil (sandy, mixed mesic, xeric torriorthent), between 1993 and 1998 (Hardegee and Van Vactor, 2000). Model simulations were run to estimate days to 50 % germination of each population of primed and non-primed seeds had they been planted on any day between 1 March and 15 May for this 6-year period. Time to germination was estimated by accumulation of °d above T_b for a given seed population subsequent to the simulated planting date. Fifty per cent germination was estimated to occur when the accumulated °d above T_b became equal to the θ estimate for that seed population (Hardegee and Van Vactor, 2000).

RESULTS

Total germination percentage was reduced by priming for some seedlots, especially at higher germination temperatures (Fig. 1). This reduction in total germination percentage was accompanied by a higher rate of fungal growth in primed seeds. It is possible that primed seeds had a higher initial level of fungus present as some fungal growth occurred on seeds during the priming treatment. Excessive fungal growth usually occurred only after some seeds in a given treatment had already died. We believe that the increased fungal growth on primed seeds was an effect rather than a cause of increased seed mortality. We attribute the reduction in total germination percentage to a reduction

in metabolic seed reserves during the priming process. Decreased seed vigour, however, was mostly seen at supra-optimal temperatures and in seedlots with the lowest initial seed vigour, i.e. Huerfano Co., CO (accession number 1105) and Douglas Co., NV (accession number 1103).

Seed priming increased the germination rate (reduced the number of days to 50 % germination) in all seedlots (Fig. 2). Huerfano Co., CO (accession number 1105) and Douglas Co., NV (accession number 1103) did not achieve 50 % germination in any of the primed treatments, but the germination rate was increased for faster-germinating seed sub-populations (data not shown). Enhancement of the germination rate was greatest at lower temperatures but there was much variability in the rate response among seedlots. At 6 °C, the lowest temperature at which all seedlots germinated during the 28 d test, days to 50 % germination was advanced by between 3.8 and 8.4 d among seedlots that achieved 50 % germination after priming. The seven *E. elymoides* seedlots germinated, on average, 7.8 ± 0.3 d sooner and the two *E. multisetus* seedlots 4.0 ± 0.3 d sooner (Fig. 2). Average decrease in germination time at 6 °C was 6.9 ± 0.6 d across all seedlots that reached 50 % germination in the primed seed treatments.

Priming decreased the base temperature for 50 % germination of all but one seedlot, with an average decrease of 1.5 ± 0.4 °C. Priming decreased the thermal time of all seedlots by between 20 and 44 °d, with an average decrease of 29 ± 2 °d (Table 2).

The thermal record from the Orchard Field Test Site between 1993 and 1998 (Fig. 3) was used to estimate days to 50 % germination for planting dates between 1 March and 15 May of each year. Figure 4 shows the mean predicted (± 1 s.e.) days to 50 % germination, across all years, as a function of planting date for primed and non-primed seedlots. For the primed seedlots that achieved 50 % germination, the simulated priming effect was maximized during cooler conditions earlier in the season. Maximum germination advancement in the model simulations was in the order of 5–10 d depending on seedlot (Fig. 4).

DISCUSSION

Total germination percentage and germination rate, or derivative indices, are often used to make treatment comparisons and to rank relative germinability of seed populations under alternative environmental conditions (Scott *et al.*, 1984; Brown and Mayer, 1988). These indices have at least two characteristics that limit their utility for making inferences about seed population response. Indices that rely on a measure of germination percentage can underestimate the response if the treatment is prematurely terminated (Romo and Eddleman, 1995); and treatment inferences are generally limited to the specific set of conditions present during a given experiment (Hurlbert, 1984). Thermal germination models generate coefficients that integrate potential response over a wide range of temperature conditions (Arnold, 1959; Garcia-Huidobro *et al.*, 1982a; Covell *et al.*, 1986; Hardegee *et al.*, 1999). These coefficients can be compared directly to rank relative potential performance of seedlots (Covell *et al.*, 1986; Ellis

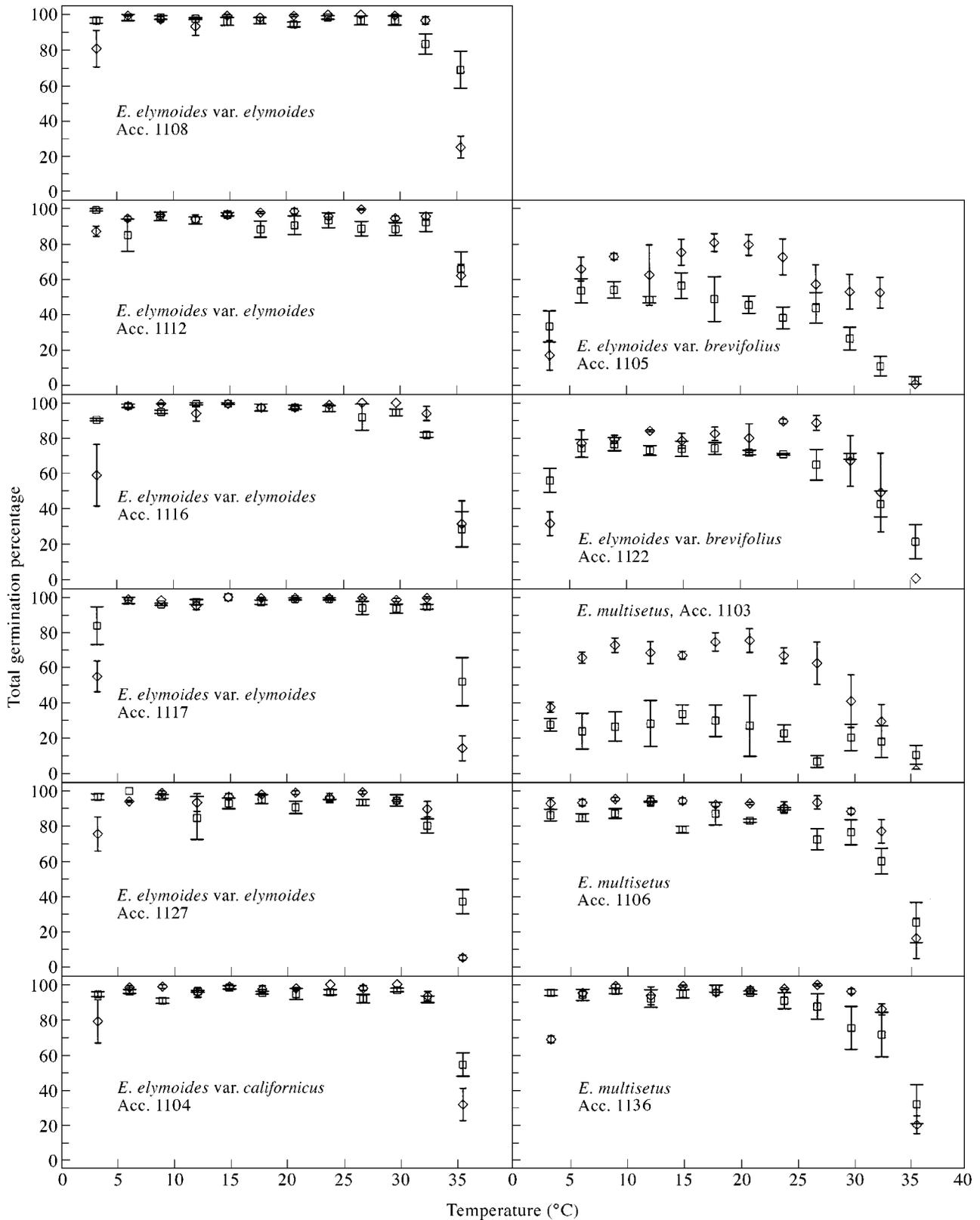


FIG. 1. Total germination percentage as a function of seedlot, priming treatment and temperature. Error bars represent ± 1 s.e. (squares, wide error bars, primed seeds; diamonds, narrow error bars, non-primed seeds).

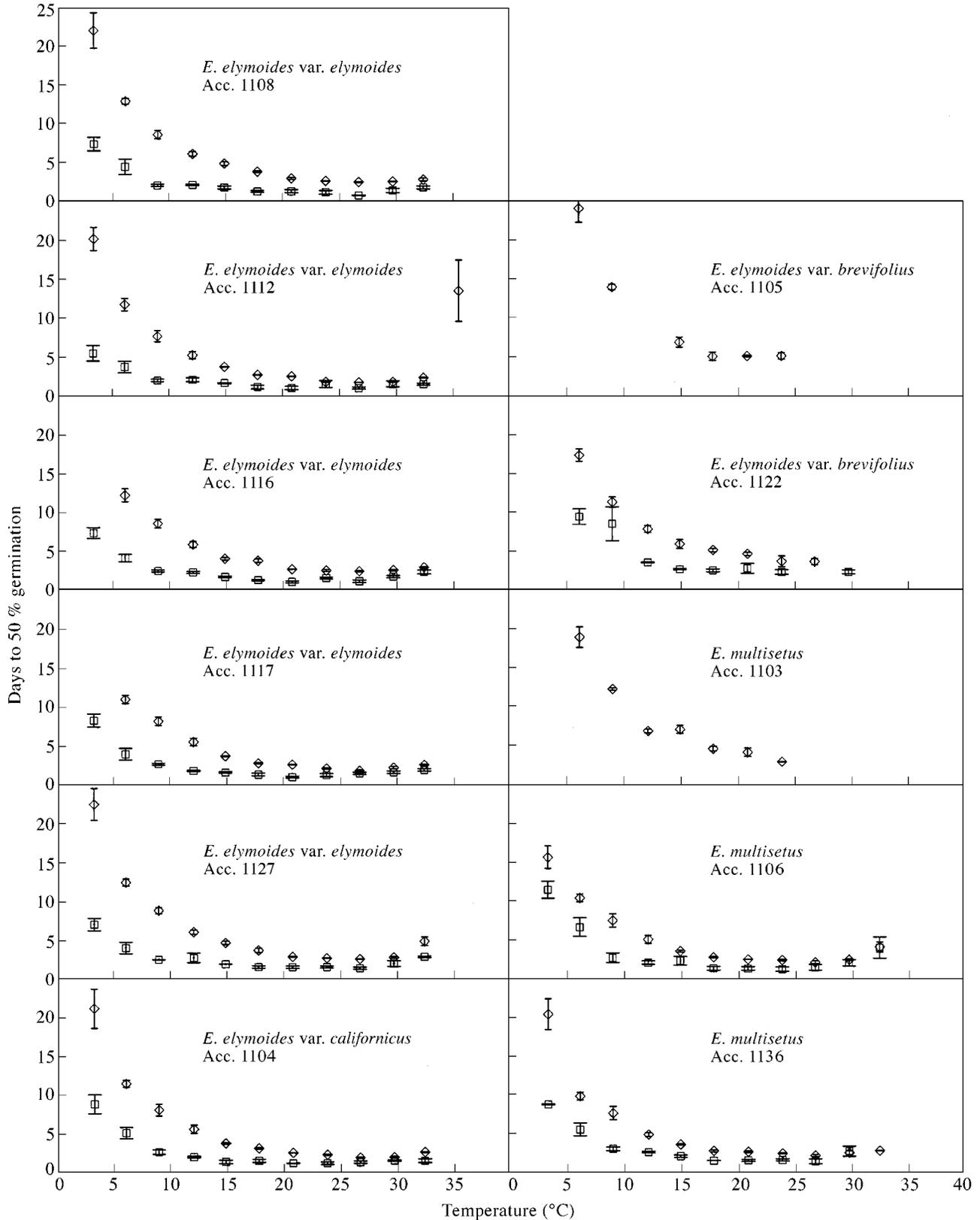


FIG. 2. Days to 50 % germination as a function of seedlot, priming treatment and temperature. Error bars represent ± 1 s.e. (squares, wide error bars, primed seeds; diamonds, narrow error bars, non-primed seeds).

TABLE 2. Thermal time and base temperature estimates for days to 50 % germination in the sub-optimal temperature range of 3–21 °C

Species	var.	Accession number	Priming treatment	Base temperature (°C)	Thermal time (°d)	Regression (r ²)
<i>E. elymoides</i>	<i>elymoides</i>	1108	Non-primed	1.5	60.2	0.97
			Primed	-1.0	25.4	0.82
<i>E. elymoides</i>	<i>elymoides</i>	1112	Non-primed	2.0	46.5	0.97
			Primed	0.1	20.2	0.75
<i>E. elymoides</i>	<i>elymoides</i>	1116	Non-primed	2.0	53.7	0.96
			Primed	1.0	20.9	0.90
<i>E. elymoides</i>	<i>elymoides</i>	1117	Non-primed	2.2	46.6	0.97
			Primed	1.3	19.1	0.90
<i>E. elymoides</i>	<i>elymoides</i>	1127	Non-primed	1.6	59.0	0.97
			Primed	-2.4	33.3	0.82
<i>E. elymoides</i>	<i>californicus</i>	1104	Non-primed	1.7	51.0	0.98
			Primed	0.1	24.4	0.80
<i>E. elymoides</i>	<i>brevifolius</i>	1105	Non-primed	2.8	84.3	0.89
			Primed	*	*	*
<i>E. elymoides</i>	<i>brevifolius</i>	1122	Non-primed	0.8	88.0	0.94
			Primed	1.0	43.5	0.79
<i>E. multisetus</i>		1103	Non-primed	2.1	77.2	0.84
			Primed	*	*	*
<i>E. multisetus</i>		1106	Non-primed	1.2	49.4	0.97
			Primed	1.1	24.1	0.73
<i>E. multisetus</i>		1136	Non-primed	1.2	50.5	0.97
			Primed	-0.3	30.9	0.93

* Treatment did not reach 50 % germination in all replicate samples.

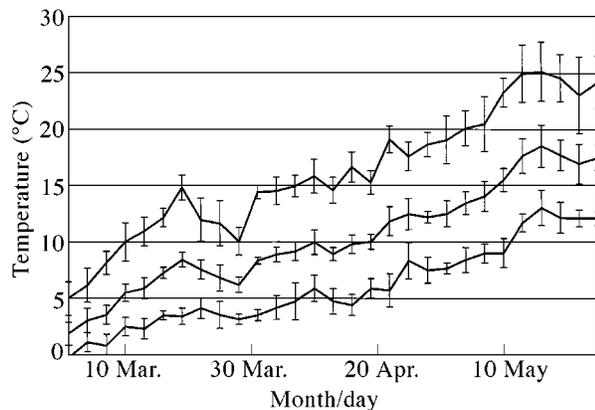


FIG. 3. Mean maximum temperature (upper line), mean minimum temperature (lower line) and mean temperature (middle line) between 1 March and 25 May for the 6-year period, 1993–1998.

et al., 1986, 1987; Jordan and Haferkamp, 1989; Fidanza *et al.*, 1996; Holshouser *et al.*, 1996) and can be validated by confirming the germination response under variable temperature conditions (Hardegree *et al.*, 1999; Hardegree and Van Vactor, 1999, 2000). Hardegree and Van Vactor (2000) suggested that such models could be used more effectively by assessing relative germination response under a broad range of alternative, simulated environmental conditions. This approach allows one to assess the probability and absolute magnitude of potential environmental response rather than just the statistical significance of treatment comparisons.

Seed priming has typically been used to enhance germination (Taylor *et al.*, 1998). Many priming studies note statistically significant priming effects, but practical efficacy is better assessed from absolute measures of field performance (Brocklehurst *et al.*, 1984; Helsel *et al.*, 1986; Alvarado *et al.*, 1987; Bradford *et al.*, 1990; Khan *et al.*, 1995; Yamamoto *et al.*, 1997). Predictive inferences from field data are limited by the specific conditions present during a given experiment (Hurlbert, 1984). Potential variability of priming response is especially difficult to assess for wild-land seeding applications because of high spatial and temporal variability in seedbed microclimate (Pierson and Wight, 1991). Hardegree and Van Vactor (2000) used thermal modelling to assess the magnitude of potential priming effects under alternative field temperature scenarios. Their analysis provided a mechanism to assess the probability of ecologically significant priming effects under a wider range of field conditions than were measured during model validation. Statistically significant priming effects in their study were not ecologically significant later in the spring when water was available and temperatures were relatively high; nor were priming effects ecologically relevant at cooler temperatures if water was not available (Hardegree and Van Vactor, 2000). Hardegree and Emmerich (1992a, b) evaluated priming effects over a wide range of experimental conditions and found that positive priming effects were limited to a relatively small set of short-duration and high water potential priming treatments. Indeed, environmental effects on subsequent germinability are usually negative unless conditions are consistently cool and dry (Roberts, 1972, 1979). Seeds can, however, be subjected to post-planting conditions that

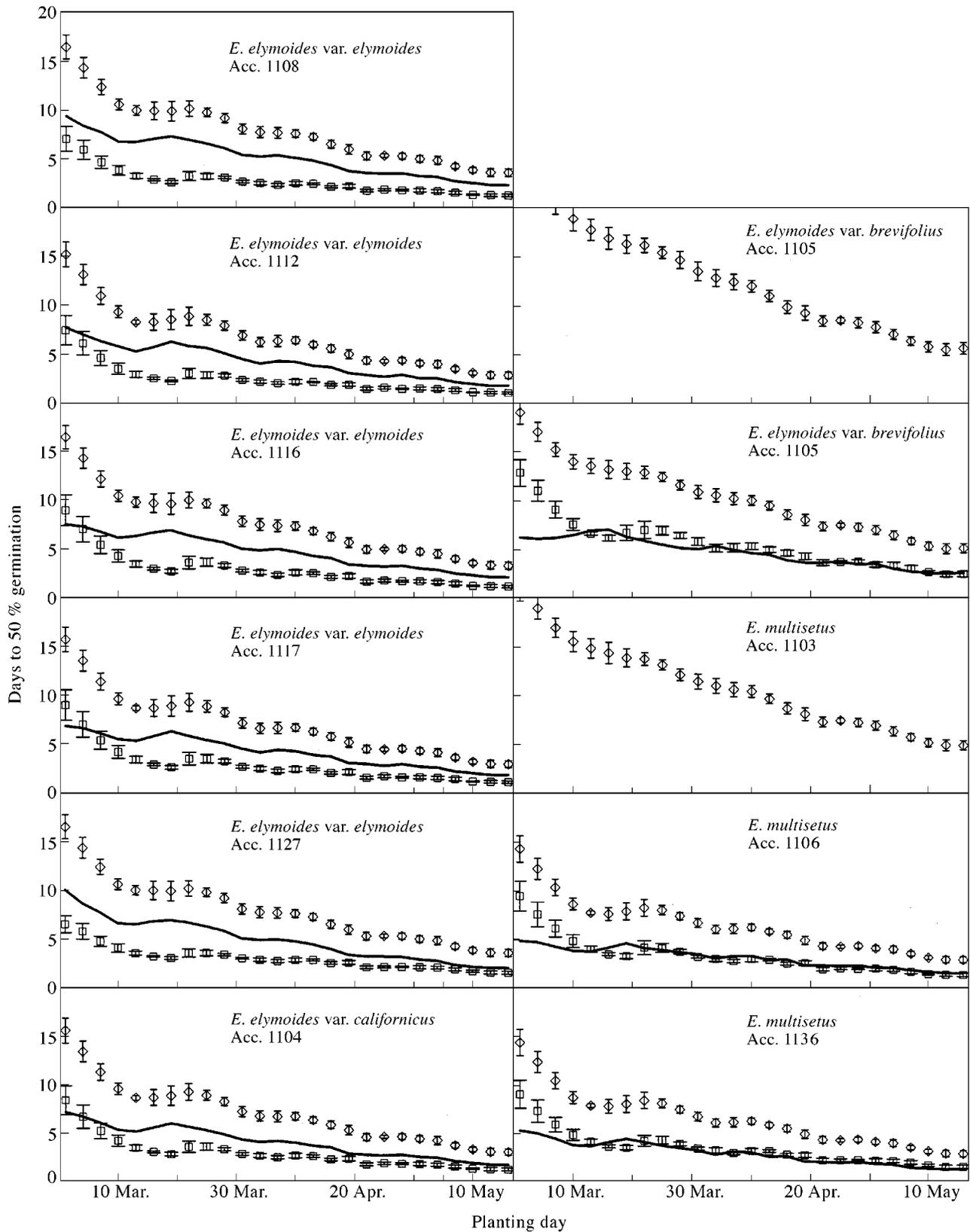


FIG. 4. Simulated mean days to 50 % germination as a function of seedlot and simulated planting date between 1 March and 15 May for the 6-year period, 1993–1998. Error bars represent ± 1 s.e. (squares, wide error bars, primed seeds; diamonds, narrow error bars, non-primed seeds). Only every third day is represented for clarity. Solid line represents the estimated difference in days to 50 % germination between non-primed and primed seeds.

improve subsequent germinability (Wallace, 1960; Lush and Groves, 1981; Lush *et al.*, 1981; Finch-Savage *et al.*, 1998; Gonzalez-Zertuche *et al.*, 2001). This is an under-investigated aspect of seed priming, especially for wild-land seeds that may be planted well in advance of conditions suitable for germination and growth. We suggest primed seed performance may also represent an upper limit to potential germinability of seeds that are not treated prior to planting. Seedlot vigour is expected to vary a great deal depending upon seed collection, processing and storage protocols. Analysis of the germination response of primed seeds may yield useful information about maximum potential field performance resulting from post-planting priming conditions in the field.

Previous studies of the thermal response of squirreltail seeds and the effects of priming (Hardegree, 1994 *a, b*, 1996; Hardegree *et al.*, 1999; Hardegree and Van Vactor, 1999, 2000; Meyer *et al.*, 2000) have not assessed variability among seedlots. Young and Evans (1977, 1982) evaluated multiple seed collections of bottlebrush squirreltail for temperature treatment effects but focused primarily on total germinability and did not model thermal response. Our data show relatively high variability in both inherent germination response and the magnitude of priming effects among seedlots (Figs 1, 2 and 4). The high variability exhibited in this experiment makes it difficult to derive any species-level inferences from our data.

Modelling and historical simulation of these data yield additional inferences that could not be evaluated by simple treatment comparisons under arbitrary temperature conditions. Figure 2 shows that priming effects are more significant at lower temperatures. Figure 4, however, also indicates the absolute magnitude and probability of significant priming effects as a function of planting date. Primed-seed response may indicate the maximum potential germination rate for these seedlots, several of which were induced to germinate more rapidly at low temperature than previously observed for this species (Hardegree, 1994 *a, b*).

These simulations assume adequate water availability subsequent to planting. More realistic simulations may require analysis of hydrothermal germination response models and evaluation relative to field variability of both temperature and water availability (Weaich *et al.*, 1996). However, Finch-Savage and Phelps (1993) and Finch-Savage *et al.* (1998) suggest that thermal response may be the primary predictor of field response above a threshold level of water availability. There are relatively few studies of hydrothermal germination response of rangeland grass species (Allen *et al.*, 2000; Meyer *et al.*, 2000). Additional research needs to be conducted to integrate both positive and negative environmental effects on germinability in the field. Christensen *et al.* (1996), Cheng and Bradford (1999) and Meyer *et al.* (2000) have noted and modelled the relationships between hydrothermal germination time, priming, and seed dormancy. Future environmental modelling will need to integrate both positive and negative impacts of seedbed temperature and moisture conditions on the germination process.

ACKNOWLEDGEMENTS

Funding was provided in part by the Bureau of Land Management, Intermountain Greenstripping and Rehabilitation Research Project, under interagency agreement USDI/BLM 60–91H2-8-0020. Mention of a trademark name or proprietary product does not constitute endorsement by the USDA and does not imply its approval to the exclusion of other products that may also be suitable.

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