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Abstract

Cheatgrass (*Bromus tectorum* L.) has come to dominate millions of hectares of rangeland in the Intermountain western United States. Previous studies have hypothesized that one mechanism conferring a competitive advantage to this species is the ability to germinate rapidly at low temperatures in the fall, winter and spring and, therefore, initiate growth and establishment more rapidly than more desirable perennial bunchgrass species. In this experiment, we developed thermal-germination-response models for multiple seedlots of cheatgrass and five perennial grass species. We conducted sensitivity analysis on potential-cumulative-germination response to a 38-y simulation of field-variable conditions of seedbed temperature and moisture. Cheatgrass uniformly germinated at a higher rate, and required significantly less time to complete germination than any of the perennial species for all but the slowest seed subpopulations. A germination-rate-sum index was used to integrate relative response characteristics over time. This index showed that germination rate of the most rapidly germinating subpopulations of cheatgrass were 2-5 times higher than for the other species tested. Model simulations of this type provide a more ecologically relevant basis for seedlot evaluation as they allow comparisons across a wide range of potential conditions that may be experienced in the field.

Introduction

Cheatgrass (*Bromus tectorum* L.) now dominates millions of hectares of sagebrush-bunchgrass rangeland in the Intermountain region of the western United States (Mack 1981; Young et al. 1987; D'Antonio and Vitousek 1992; Knapp 1996; DiTomaso 2000). It has been suggested that rapid germination, particularly at low temperatures in the late fall, winter and early spring, may contribute to the competitive success of this species (Hull 1964; Harris 1967; Harris and Wilson 1970; Wilson et al. 1974; Harris 1977; Thill et al. 1979; Hardegree 1994a,b; Beckstead et al. 1996; Goodwin et al. 1996; Hardegree et al. 2003). Young and Evans (1982) evaluated thermal response of a large number of seedlots of cheatgrass and other species, under a wide variety of thermal conditions, but only reported temperature effects on total germination percentage. Several previous studies have evaluated thermal or hydrothermal-germination response of cheatgrass and other rangeland grasses, but limited analysis to comparison of model indices, or focused on seed-dormancy processes (Wester 1991; Jordan and Haferkamp 1989; Hardegree 1994a,b; Romo and Eddleman 1995; Allen et al. 2000; Meyer et al., 2000). Hardegree and Van Vactor (2000) and Hardegree et al. (2003) proposed that model estimates of cumulative germination response to potential field-variable temperature and moisture regimes might provide a more ecologically relevant index for species and seedlot

comparisons. Hardegree et al. (2008) evaluated thermal-germination response of 41 accessions of bottlebrush squirreltail [*Elymus elymoides* (Raf.) Swezey] and big squirreltail [*Elymus multisetus* (J.G. Smith) Burtt-Davy] using this methodology and Roundy et al. (2007) used a similar approach to evaluate potential germination response of 18 cheatgrass seedlots over a four-year period at nine big sagebrush (*Artemisia tridentata* Nutt.) sites in Nevada and Utah. Historical simulation of potential germination response can be used to rank seedlots, but also provides sensitivity analysis on the effects of annual and seasonal variability in temperature and water conditions that may be experienced in the field (Hardegree 2006b).

The purpose of the current study was to expand upon previous analyses of Hardegree et al. (2003), Roundy et al. (2007) and Hardegree et al. (2008) to include multiple accessions of cheatgrass, big and bottlebrush squirreltail, bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) Löve], basin wildrye [*Leymus cinereus* (Scribn. and Merr.) A. Löve] and Sandberg bluegrass (*Poa secunda* Vasey). Specific objectives were to compare simulated germination rate of cheatgrass and perennial-bunchgrass species under historical field-temperature regimes; and to evaluate potential variability in cumulative germination response as a function of seasonal and annual variability in seedbed temperature and moisture.

Methods

Thermal germination-response data for 23 seedlots of bottlebrush squirreltail, 20 seedlots of big squirreltail, eight seedlots of cheatgrass, three seedlots of bluebunch wheatgrass, and one seedlot of Sandberg bluegrass, were derived from several previous studies as described by Hardegree et al. (2003), Hardegree (2006a), Roundy et al. (2007) and Hardegree et al. (2008).

Five additional seedlots of bluebunch wheatgrass; five seedlots of basin wildrye, four seedlots of bottlebrush squirreltail and one seedlot of big squirreltail were harvested from nursery-grown plants at the Utah State University, Evans Farm, Millville, UT in 1996 for germination testing in 1997. The cultural practices for seed production followed similar procedures described by Jones et al. (2003) for big and bottlebrush squirreltail. The five seedlots of basin wildrye originated from two released varieties (Trailhead and Magnar) and three wildland collections (Benson, UT; Soda Springs, ID; Delcio, NV). The additional seedlots of bluebunch wheatgrass also originated from two released varieties (Whitmar and Goldar) and three wildland collections (Ainsworth BC, Connell, WA, and Meeker, CO). The four additional accessions of bottlebrush squirreltail and one accession of big squirreltail were derived from wildland collections (*E. elymoides* ssp. *brevifolius* from Buford, CO, Pueblo, CO and Los Lunas, NM; *E. elymoides* ssp. *elymoides* from Ten Sleep, WY; *E. multisetus* from Sand Hollow, ID). The three *E. elymoides* ssp. *brevifolius* accessions belonged to Group A as identified by Jones et al. (2003) and Hardegree et al. (2008). The Ainsworth BC collection of bluebunch wheatgrass, and Sand Hollow, ID collection of bottlebrush squirreltail, were the same as two previous accessions included from the previous study by Hardegree et al. (2003).

Twenty-one constant-temperature regimes between 3 and 38°C were tested for the 15 additional seedlots using a similar experimental design described by Hardegree (2006a). Germination vials, containing 30 seeds each, were replicated 5 times within each environmental chamber but individual temperature regimes were not replicated. Seeds were monitored every day, for up to 52 days in some of the colder temperature treatments, and were counted and removed when they exhibited radicle extension of $\geq$ 2 mm.

One additional seedlot of Sandberg bluegrass was obtained from a commercial seed company and evaluated for thermal-germination response in 2007 using the same general experimental design described by Roundy et al. (2007) for cheatgrass seedlots, except that germination vials were replicated 4 times within each chamber.

The statistical-gridding (SG) procedure developed by Hardegree and Winstral (2006) and tested by Hardegree (2006b) was used to model germination rate (d-1) for each seedlot as a function of temperature and seed-subpopulation. Germination-rates as a function of temperature for all subpopulations (5-95% in 5% increments) of each seedlot were estimated for each hour of a 255-d period between 6-Oct and 18-Jun of a given hydrologic year for a 38-year seedbed-microclimatic simulation as previously described by Hardegree et al. (2003). This process was repeated for all hours of the test period regardless of simulated soil-water potential (Flerchinger and Hardegree 2004) as described by Hardegree et al. (2008). Under a second scenario, germination rates were estimated only for hours in which water potential was estimated to be less negative than -1.0 MPa (Hardegree et al. 2003; Roundy et al. 2007). These hourly-rate estimates reflect the percentage progress toward germination of a given subpopulation during each hour. The summation of hourly-rate values over a 24-hour period, therefore, represents the percentage

progress toward germination for a given day, therefore, germination time can be estimated as the time it takes for the cumulative-germination- rate sum to become equal to 1 (Roundy and Biedenbender 1996; Phelps and Finch-Savage 1997; Hardegree et al. 1999).

Germination-rate sums were calculated for each combination of species, accession, seedlot-collection year, and subpopulation for every day of the 255-day simulation period for each year. Germination time was also calculated for every subpopulation for 12 simulated planting dates in each year starting on Oct-9 and every 21-days thereafter until 28-May. The last 8 simulated planting dates in this study were identical to those described by Hardegree et al. (2008) for 41 squirreltail seedlots. Rate-sums and germination-times were averaged across seedlot accessions that were collected in different years, and then averaged across all years of the test period by Julian date. Mean rate sums for a given Julian date and seedlot-accession were then averaged by species for cheatgrass, bluebunch wheatgrass, basin wildrye, Sandberg bluegrass, and big squirreltail; and by subspecies grouping for bottlebrush squirreltail (ssp. *brevifolius* Group A; ssp. *brevifolius* Group B; ssp. *brevifolius* Group C; ssp. *elymoides*) as identified by Jones et al. (2003) and Hardegree et al. (2008). The 5 seedlots of basin wildrye exhibited two distinct groupings based on relative population response and were divided into two categories: released varieties (Trailhead and Magnar) and wildland collections (Benson, UT; Soda Springs, ID; Delcio, NV).

Species and subspecies seedlot-groupings were compared for relative germination response using mixed-model Analysis of Variance (ANOVA) for: comparison of daily-rate sums on the 12 simulated planting dates; comparison of annual rate-sums accumulated over the entire 255-d evaluation period; and comparison of germination time as a function of simulated planting date for model simulations using all hourly temperatures, and for model simulations in which thermal-accumulation was only calculated when simulated soil water potential was less negative than -1.0 MPa. Daily and annual-rate sums, and germination-time values were only evaluated for select subpopulations (10%, 30%, 50% and 70%). The Fisher's protected least-square-difference test was used for multiple comparisons of significant main-treatment effects.

Results

The seasonal distribution of daily-germination rate-sums, as affected by temperature only, is shown in Figure 1. The vertical lines in this figure correspond to the 12 simulated planting dates. Species and subspecies groupings were roughly ranked based on maximum-daily rate-sum of the 50% subpopulation in the following order of relative germination rate (high to low): cheatgrass > bluebunch wheatgrass, big squirreltail > bottlebrush squirreltail ssp. *brevifolius* Group C > bottlebrush squirreltail ssp. *brevifolius* Groups A,B; bottlebrush squirreltial ssp. *elymoides* > Sandberg bluegrass > basin wildrye (wildand collections) > basin wildrye (released varieties). The results of the multiple-comparison test for significant differences among species groupings is shown in Table 1 for the 30% subpopulation for selected planting dates. Significant differences in daily rate-sums were dependent upon both planting date and subpopulation. Results of significance testing for other subpopulations and planting dates can be reviewed on-line at: http://... . Data for subpopulation variability in daily thermal-rate summation shows a consistent and expected pattern of seasonal variability across all species. Daily-germination rate-sum estimates were reduced by approximately 2/3 when thermal accumulation was limited to periods when water potential was estimated to be less negative than -1.0 MPa (Fig. 2), but relative seedlot response and differences among seedlots was similar (Table 2; http://...).

The mean annual-cumulative-rate-sum as a function of seed subpopulation during the 255-d test period is shown for all seedlot groups in Figure 3. The cumulative rate-sum shown in this figure integrates the data in Fig. 1 to provide a more concise index for comparison of species and seedlot differences. As with the daily-rate-sum data, significance of species and seedlot differences were subpopulation dependant (Table 3; http://...). In general, Cheatgrass germination rates were 2-5 times higher than for the other species for the most rapidly germinating subpopulations, but were similar for all species for slower-germinating seed subpopulations (Figs. 1, 2, 3). An alternative way to interpret the data in Fig. 3 is to consider that the numerical value of the cumulative-rate-sum is equivalent to the number of times a given subpopulation would be expected to germinate if planted sequentially, immediately after germination occurred from the previous planting event. The data in Figure 3 overestimate the number of periods in which germination would be expected to occur as they do not take into account water-potential effects. The equivalent data for thermal accumulation above the -1.0 MPa water-potential threshold were of the same relative magnitude, but approximately 1/3 the magnitude of the values for the data shown in Fig. 3 (Data not shown).

Patterns of cumulative germination matched the rate-sum data but differences in seedlot groupings were highly dependant on planting date (Figure 4, Table 4; http://...). Simulated germination times for the 50%-seed subpopulation ranged from about 50-100 days for most seedlot groupings for simulated planting dates in early December, to only 3-10 days in late May (Fig. 4a). Simulated germination times were greatly delayed when thermal accumulation was restricted to periods of relative water availability (Fig. 4b). This delay was relatively greater during warmer planting periods when the seeds were more likely to experience water stress.

Discussion

Wester (1991) summarized the results of many previous studies investigating temperature and water-stress effects on rangeland-plant germination. The majority of these studies evaluated only a limited number of static treatment effects, and did not address species-level variability in germination response. Young and Evans (1981; 1982), Evans and Young (1983), Evans et al. (1977), and Young et al. (1981; 2003), measured germination response of a large number of rangeland grass species to a wide range of constant and alternating-temperature regimes, but reported only total germination response. Young and Evans (1977) and Kitchen and Monsen (1994) reported thermal effects on rate as well as total germination percentage of squirreltail and bluebunch wheatgrass, respectively, but used a rate index that is confounded by differences in germination percentage (Scott et al. 1984; Brown and Mayer 1988). Thermal and hydrothermal models have been used to generate rate indices integrating potential response over a wide range of environmental conditions but most previous comparisons for rangeland species have been limited to simple ranking of thermal or hydrothermal coefficients (Jordan and Haferkamp 1989; Allen et al. 2000; Meyer et al. 2000). Hardegree and Van Vactor (2000) and Hardegree et al. (2003) suggested that thermal and hydrothermal germination models could be used in conjunction with measured or simulated microclimatic data to develop a more ecologically relevant basis for seedlot and species comparisons. Hardegree et al. (2003) and Hardegree (2006b) used this approach to simulate germination response to historical conditions of seedbed moisture and temperature, but only for one or two seedlots of a given species. Roundy et al. (2007) evaluated potential germination response to field-variable microclimatic conditions but limited analysis to evaluation of single species. Hardegree et al. (2008) is the only study of this type that has compared more than two seedlots of different species (big and bottlebrush squirreltail). The current study included re-analysis of these previous studies (Hardegree et al. 2003; Hardegree 2006b; Roundy et al. 2007; Hardegree et al. 2008) but expanded the comparison to include an expanded range of simulated planting dates, and new data for additional species and seedlots. The current study also included consideration of a water-potential threshold for thermal accumulation as discussed by Hardegree et al. (2003) and Roundy et al. (2008).

The results in this study confirm previous assertions that cheatgrass exhibits superior germination response to many perennial grass species, especially under conditions of low temperature in the late fall, winter and early spring (Hull 1964; Harris 1967; Harris and Wilson 1970; Wilson et al. 1974; Harris 1977; Thill et al. 1979; Hardegree 1994a,b; Beckstead et al. 1996; Goodwin et al. 1996; Hardegree et al. 2003). Our model simulations predicted relatively similar germination rates during the coolest part of the year (Figs. 1,2). Small germination-rate differences, however, are magnified when the inverse of rate is calculated to estimate actual germination time (Fig. 4), a more relevant basis for comparison of potential field performance (Arnold, 1959).

Several assumptions were made in this analysis that could affect interpretation of the simulated germination response. Assumptions inherent in thermal-germination models *per se* are thoroughly discussed by Hardegree et al. (1999). These assumptions were minimized for the statistical-gridding model used in the current experiment as developed and tested by Hardegree (2006a,b) and Hardegree and Winstral (2006). Additional assumptions were made in the application of the water-potential threshold concept first applied in a modeling context by Roundy et al. (2007). Hardegree et al. (2003) assessed the relative importance of different water-potential thresholds, however, and Roundy et al. (2007) confirmed that a threshold of -1.0 MPa would be expected to explain the majority of periods during which wet-thermal accumulation toward germination would be expected to occur. Additional studies should be conducted to confirm this methodology with additional species and seedlots using hydrothermal germination-response data.

Many important biotic and abiotic factors that affect germination response and subsequent emergence, growth and establishment in the field were also ignored in this analysis (Hegarty 1973; Egli and Tekrony 1996; Weaich et al. 1996; Beckstead et al. 2007). More rapid germination of cheatgrass is also only one component of a competitive syndrome that includes rapid root and shoot growth (Hull 1963; Harris 1967; Harris 1977; Link et al. 1990; Svejcar 1990; Aguirre and Johnson 1991; Nasri and Doescher 1995; Arredondo and Johnson 1998; Arredondo et al. 1998),

high seed production (Young et al. 1969; Humphrey and Schupp 2001; Hempy-Mayer and Pyke 2008), resource exclusion through efficient water utilization, especially in the upper soil layers (Evans et al. 1970; Cline et al. 1977; Melgoza et al. 1990; Booth et al. 2003a; Humphrey and Schupp 2004), alteration of the fire cycle (Whisenant 1990; Knapp 1996), and changes in nitrogen dynamics (Evans et al. 2001; Booth et al. 2003b; Rimer and Evans 2006). We believe, however, that this modeling approach yields a much higher level of ecologically relevant information than previous methods, and that this information could be used to identify relevant germination syndromes (Angevine and Chabot 1979; Humphrey and Schupp 1999) rather than merely ranking relative species response.

Management Implications

Methodologies discussed in this study provide a more ecologically relevant basis for comparison of thermal and water-potential effects on seed-germination response than previous approaches. Assessment of potential germination response to a wide number of potential field conditions expands relevant comparisons of species and seedlots to specifically include consideration of the impacts of highly stochastic weather and climate variables as moderated by the seedbed. Future utilization of these techniques could lead to classification of hydrothermal-germination syndromes but could also be used to develop a system for ranking sites and years based on relative favorability of seedbed microclimate. This type of tool would greatly assist in the interpretation of alternative seeding treatments and in quantification of climatic influences on establishment success. Methodology for evaluating weather and climate impacts on establishment success would also provide a basis for interpreting potential climate-change impacts on the stability of current plant communities.

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FIGURES

Figure 1. Seasonal variability in mean daily-rate-sum as a function of seed subpopulation and seedlot group for *Bromus tectorum* (▴), *Elymus multisetus* (◇), *Pseudoroegneria spicata* (▽), *Elymus elymoides* ssp. *brevifolius* Group C (▾), *Elymus elymoides* ssp. *brevifolius* Group B (□), *Elymus elymoides* ssp. *elymoides* (△), *Elymus elymoides* ssp. *brevifolius* Group A (○), *Leymus cinereus* wildland collections (closed octagon), *Poa secunda* (♦), and *Leymus cinereus* released varieties (☆). Daily-rate-sum means were derived by first averaging by seedlot across all years, and then across seedlots within groups. Rate-sum means in this figure were calculated for all hours regardless of water potential estimate. Vertical lines on x-axis represent simulated planting dates.

Figure 2. Seasonal variability in mean daily-rate-sum as a function of seed subpopulation and seedlot group for *Bromus tectorum* (▴), *Elymus multisetus* (◇), *Pseudoroegneria spicata* (▽), *Elymus elymoides* ssp. *brevifolius* Group C (▾), *Elymus elymoides* ssp. *brevifolius* Group B (□), *Elymus elymoides* ssp. *elymoides* (△), *Elymus elymoides* ssp. *brevifolius* Group A (○), *Leymus cinereus* wildland collections (closed octagon), *Poa secunda* (♦), and *Leymus cinereus* released varieties (☆). Daily-rate-sum means were derived by first averaging by seedlot across all years, and then across seedlots withing groups. Rate-sum means in this figure were calculated only for hours where the water potential was less negative than -1.0 MPa. Vertical lines on x-axis represent simulated planting dates.

Figure 3. Annual-cumulative-rate sums for the 255-day test period as a function of seed subpopulation and seedlot-group for *Bromus tectorum* (▲), *Elymus multisetus* (◇), *Pseudoroegneria spicata* (▽), *Elymus elymoides* ssp. *brevifolius* Group C (▼), *Elymus elymoides* ssp. *brevifolius* Group B (□), *Elymus elymoides* ssp. *elymoides* (△), *Elymus elymoides* ssp. *brevifolius* Group A (○), *Leymus cinereus* wildland collections (closed octagon), *Poa secunda* (♦), and *Leymus cinereus* released varieties (☆). Vertical lines indicate the subpopulations used in the ANOVA and multiple comparison procedures.

Figure 4. Mean-predicted cumulative germination response as a function of selected planting dates using all temperature data (4a) and temperature data only for hours where the water potential was estimated to be less negative than -1.0 MPa (4b) for *Bromus tectorum* (▲), *Elymus multisetus* (◇), *Pseudoroegneria spicata* (▽), *Elymus elymoides* ssp. *brevifolius* Group C (▼), *Elymus elymoides* ssp. *brevifolius* Group B (□), *Elymus elymoides* ssp. *elymoides* (△), *Elymus elymoides* ssp. *brevifolius* Group A (○), *Leymus cinereus* wildland collections (closed octagon), *Poa secunda* (♦), and *Leymus cinereus* released varieties (☆).

Table 1. Significance matrix for individual comparisons of mean-daily-germination-rate-sums for thermal accumulation across all water potentials as a function of seedlot-goup pair and selected planting dates for the 30% seed subpopulation. Each seedlot-goup is arranged in order of relative germination-rate to facilitate general comparisons. Significant (S) and non-significant (NS) treatment comparisons were determined using the Fisher's protected least-square-difference test for significant main-treatment effects. Brte (*Bromus tectorum*), Elmu (*Elymus multisetus*), Pssp (*Pseudoroegneria spicata*), ElelC (*Elymus elymoides* ssp. *brevifolius* Group C), ElelB (*Elymus elymoides* ssp. *brevifolius* Group B), Elel (*Elymus elymoides* ssp. *elymoides*), ElelA (*Elymus elymoides* ssp. *brevifolius* Group A), Pose (*Poa secunda*), LeciW (*Leymus cinereus* wildland collections varieties), LeciR (*Leymus cinereus* released varieties).

| | Planting Date | | | | | | | Planting Date | | | | | |
Species	30-Oct	11-Dec	22-Jan	05-Mar	16-Apr	28-May	Species	30-Oct	11-Dec	22-Jan	05-Mar	16-Apr	28-May
Brte v. Elmu	S	S	NS	S	S	S	Elel v. Brte	S	S	S	S	S	S
Brte v. Pssp	S	S	S	S	S	S	Elel v. Elmu	S	S	S	S	S	S
Brte v. ElelC	S	S	S	S	S	S	Elel v. Pssp	S	NS	NS	S	S	NS
Brte v. ElelB	S	S	S	S	S	S	Elel v. ElelC	NS	NS	NS	NS	NS	NS
Brte v. Elel	S	S	S	S	S	S	Elel v. ElelB	NS	NS	NS	NS	NS	NS
Brte v. ElelA	S	S	S	S	S	S	Elel v. ElelA	NS	NS	NS	NS	NS	NS
Brte v. Pose	S	S	S	S	S	S	Elel v. Pose	NS	NS	NS	NS	NS	NS
Brte v. LeciW	S	S	S	S	S	S	Elel v. LeciW	NS	NS	NS	NS	NS	NS
Brte v. LeciR	S	S	S	S	S	S	Elel v. LeciR	S	S	S	S	S	S
Elmu v. Brte	S	S	NS	S	S	S	ElelA v. Brte	S	S	S	S	S	S
Elmu v. Pssp	S	S	S	S	NS	NS	ElelA v. Elmu	S	S	S	S	S	S
Elmu v. ElelC	S	S	S	S	NS	NS	ElelA v. Pssp	S	S	S	S	S	S
Elmu v. ElelB	S	S	S	S	S	NS	ElelA v. ElelC	NS	NS	NS	NS	S	S
Elmu v. Elel	S	S	S	S	S	S	ElelA v. ElelB	NS	NS	NS	NS	NS	NS
Elmu v. ElelA	S	S	S	S	S	S	ElelA v. Elel	NS	NS	NS	NS	NS	NS
Elmu v. Pose	S	S	S	S	S	S	ElelA v. Pose	NS	NS	NS	NS	NS	NS
Elmu v. LeciW	S	S	S	S	S	S	ElelA v. LeciW	NS	NS	NS	NS	NS	NS
Elmu v. LeciR	S	S	S	S	S	S	ElelA v. LeciR	S	S	S	S	S	S

Table 2. (continued)

	1	2	3	4	5	6		1	2	3	4	5	6
Pssp v. Brte	S	S	S	S	S	S	Pose v. Brte	S	S	S	S	S	S
Pssp v. Elmu	S	S	S	S	NS	NS	Pose v. Elmu	S	S	S	S	S	S
Pssp v. ElelC	NS	S	S	NS	NS	NS	Pose v. Pssp	S	S	S	S	S	S
Pssp v. ElelB	NS	NS	NS	NS	NS	NS	Pose v. ElelC	NS	NS	NS	NS	S	NS
Pssp v. Elel	S	NS	NS	S	S	NS	Pose v. ElelB	NS	NS	NS	NS	NS	NS
Pssp v. ElelA	S	S	S	S	S	S	Pose v. Elel	NS	NS	NS	NS	NS	NS
Pssp v. Pose	S	S	S	S	S	S	Pose v. ElelA	NS	NS	NS	NS	NS	NS
Pssp v. LeciW	S	S	S	S	S	S	Pose v. LeciW	NS	NS	NS	NS	NS	NS
Pssp v. LeciR	S	S	S	S	S	S	Pose v. LeciR	S	S	NS	S	S	NS
ElelC v. Brte	S	S	S	S	S	S	LeciW v. Brte	S	S	S	S	S	S
ElelC v. Elmu	S	S	S	S	NS	NS	LeciW v. Elmu	S	S	S	S	S	S
ElelC v. Pssp	NS	S	S	NS	NS	NS	LeciW v. Pssp	S	S	S	S	S	S
ElelC v. ElelB	NS	NS	NS	NS	NS	NS	LeciW v. ElelC	S	NS	NS	S	S	NS
ElelC v. Elel	NS	NS	NS	NS	NS	NS	LeciW v. ElelB	NS	NS	NS	NS	NS	NS
ElelC v. ElelA	NS	NS	NS	NS	S	S	LeciW v. Elel	NS	NS	NS	NS	NS	NS
ElelC v. Pose	NS	NS	NS	NS	S	NS	LeciW v. ElelA	NS	NS	NS	NS	NS	NS
ElelC v. LeciW	S	NS	NS	S	S	NS	LeciW v. Pose	NS	NS	NS	NS	NS	NS
ElelC v. LeciR	S	S	S	S	S	S	LeciW v. LeciR	S	NS	NS	S	S	S
ElelB v. Brte	S	S	S	S	S	S	LeciR v. Brte	S	S	S	S	S	S
ElelB v. Elmu	S	S	S	S	S	NS	LeciR v. Elmu	S	S	S	S	S	S
ElelB v. Pssp	NS	NS	NS	NS	NS	NS	LeciR v. Pssp	S	S	S	S	S	S
ElelB v. ElelC	NS	NS	NS	NS	NS	NS	LeciR v. ElelC	S	S	S	S	S	S
ElelB v. Elel	NS	NS	NS	NS	NS	NS	LeciR v. ElelB	S	S	S	S	S	S
ElelB v. ElelA	NS	NS	NS	NS	NS	NS	LeciR v. Elel	S	S	S	S	S	S
ElelB v. Pose	NS	NS	NS	NS	NS	NS	LeciR v. ElelA	S	S	S	S	S	S
ElelB v. LeciW	NS	NS	NS	NS	NS	NS	LeciR v. Pose	S	S	NS	S	S	NS
ElelB v. LeciR	S	S	S	S	S	S	LeciR v. LeciW	S	NS	NS	S	S	S

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Table 2. Significance matrix for individual comparisons of mean-daily-germination-rate-sums for thermal accumulation for water potentials less negative than -1.0 MPa as a function of seedlot-goup pair and selected planting dates for the 30% seed subpopulation. Each seedlot-gourp is arranged in order of relative germination-rate to facilitate general comparisons. Significant (S) and non-significant (NS) treatment comparisons were determined using the Fisher's protected least-square-difference test for significant main-treatment effects. Brte (*Bromus tectorum*), Elmu (*Elymus multisetus*), Pssp (*Pseudoroegneria spicata*), ElelC (*Elymus elymoides* ssp. *brevifolius* Group C), ElelB (*Elymus elymoides* ssp. *brevifolius* Group B), Elel (*Elymus elymoides* ssp. *elymoides*), ElelA (*Elymus elymoides* ssp. *brevifolius* Group A), Pose (*Poa secunda*), LeciW (*Leymus cinereus* wildland collections), LeciR (*Leymus cinereus* released varieties).

Species	Planting Date						Species	Planting Date					
	30-Oct	11-Dec	22-Jan	05-Mar	16-Apr	28-May		30-Oct	11-Dec	22-Jan	05-Mar	16-Apr	28-May
Brte v. Elmu	S	S	NS	S	S	S	Elel v. Brte	S	S	S	S	S	S
Brte v. Pssp	S	S	S	S	S	S	Elel v. Elmu	S	S	S	S	S	S
Brte v. ElelC	S	S	S	S	S	S	Elel v. Pssp	S	NS	NS	S	S	NS
Brte v. ElelB	S	S	S	S	S	S	Elel v. ElelC	NS	NS	NS	NS	NS	NS
Brte v. Elel	S	S	S	S	S	S	Elel v. ElelB	NS	NS	NS	NS	NS	NS
Brte v. ElelA	S	S	S	S	S	S	Elel v. ElelA	NS	NS	NS	NS	NS	NS
Brte v. Pose	S	S	S	S	S	S	Elel v. Pose	NS	NS	NS	NS	NS	NS
Brte v. LeciW	S	S	S	S	S	S	Elel v. LeciW	NS	NS	NS	NS	NS	NS
Brte v. LeciR	S	S	S	S	S	S	Elel v. LeciR	S	S	S	S	S	S
Elmu v. Brte	S	S	NS	S	S	S	ElelA v. Brte	S	S	S	S	S	S
Elmu v. Pssp	S	S	S	S	NS	NS	ElelA v. Elmu	S	S	S	S	S	S
Elmu v. ElelC	S	S	S	S	NS	NS	ElelA v. Pssp	S	S	S	S	S	S
Elmu v. ElelB	S	S	S	S	S	NS	ElelA v. ElelC	NS	NS	NS	NS	S	S
Elmu v. Elel	S	S	S	S	S	S	ElelA v. ElelB	NS	NS	NS	NS	NS	NS
Elmu v. ElelA	S	S	S	S	S	S	ElelA v. Elel	NS	NS	NS	NS	NS	NS
Elmu v. Pose	S	S	S	S	S	S	ElelA v. Pose	NS	NS	NS	NS	NS	NS
Elmu v. LeciW	S	S	S	S	S	S	ElelA v. LeciW	NS	NS	NS	NS	NS	NS
Elmu v. LeciR	S	S	S	S	S	S	ElelA v. LeciR	S	S	S	S	S	S

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Table 2. (continued)

Pssp v. Brte	S	S	S	S	S	S	Pose v. Brte	S	S	S	S	S	S
Pssp v. Elmu	S	S	S	S	NS	NS	Pose v. Elmu	S	S	S	S	S	S
Pssp v. ElelC	NS	S	S	NS	NS	NS	Pose v. Pssp	S	S	S	S	S	S
Pssp v. ElelB	NS	NS	NS	NS	NS	NS	Pose v. ElelC	NS	NS	NS	NS	S	NS
Pssp v. Elel	S	NS	NS	S	S	NS	Pose v. ElelB	NS	NS	NS	NS	NS	NS
Pssp v. ElelA	S	S	S	S	S	S	Pose v. Elel	NS	NS	NS	NS	NS	NS
Pssp v. Pose	S	S	S	S	S	S	Pose v. ElelA	NS	NS	NS	NS	NS	NS
Pssp v. LeciW	S	S	S	S	S	S	Pose v. LeciW	NS	NS	NS	NS	NS	NS
Pssp v. LeciR	S	S	S	S	S	S	Pose v. LeciR	S	S	NS	S	S	NS
ElelC v. Brte	S	S	S	S	S	S	LeciW v. Brte	S	S	S	S	S	S
ElelC v. Elmu	S	S	S	S	NS	NS	LeciW v. Elmu	S	S	S	S	S	S
ElelC v. Pssp	NS	S	S	NS	NS	NS	LeciW v. Pssp	S	S	S	S	S	S
ElelC v. ElelB	NS	NS	NS	NS	NS	NS	LeciW v. ElelC	S	NS	NS	S	S	NS
ElelC v. Elel	NS	NS	NS	NS	NS	NS	LeciW v. ElelB	NS	NS	NS	NS	NS	NS
ElelC v. ElelA	NS	NS	NS	NS	S	S	LeciW v. Elel	NS	NS	NS	NS	NS	NS
ElelC v. Pose	NS	NS	NS	NS	S	NS	LeciW v. ElelA	NS	NS	NS	NS	NS	NS
ElelC v. LeciW	S	NS	NS	S	S	NS	LeciW v. Pose	NS	NS	NS	NS	NS	NS
ElelC v. LeciR	S	S	S	S	S	S	LeciW v. LeciR	S	NS	NS	S	S	S
ElelB v. Brte	S	S	S	S	S	S	LeciR v. Brte	S	S	S	S	S	S
ElelB v. Elmu	S	S	S	S	S	NS	LeciR v. Elmu	S	S	S	S	S	S
ElelB v. Pssp	NS	NS	NS	NS	NS	NS	LeciR v. Pssp	S	S	S	S	S	S
ElelB v. ElelC	NS	NS	NS	NS	NS	NS	LeciR v. ElelC	S	S	S	S	S	S
ElelB v. Elel	NS	NS	NS	NS	NS	NS	LeciR v. ElelB	S	S	S	S	S	S
ElelB v. ElelA	NS	NS	NS	NS	NS	NS	LeciR v. Elel	S	S	S	S	S	S
ElelB v. Pose	NS	NS	NS	NS	NS	NS	LeciR v. ElelA	S	S	S	S	S	S
ElelB v. LeciW	NS	NS	NS	NS	NS	NS	LeciR v. Pose	S	S	NS	S	S	NS
ElelB v. LeciR	S	S	S	S	S	S	LeciR v. LeciW	S	NS	NS	S	S	S

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Table 3. Significance matrix for individual comparisons of annual-cumulative-rate-sums as a function seedlot-gourp pair and selected subpopulations. Each seedlot-group is arranged in order of relative germination-rate to facilitate general comparisons. Significant (S) and non-significant (NS) treatment comparisons were determined using the Fisher's protected least-square-difference test for significant main-treatment effects. Brte (*Bromus tectorum*), Elmu (*Elymus multisetus*), Pssp (*Pseudoroegneria spicata*), ElelC (*Elymus elymoides* ssp. *brevifolius* Group C), ElelB (*Elymus elymoides* ssp. *brevifolius* Group B), Elel (*Elymus elymoides* ssp. *elymoides*), ElelA (*Elymus elymoides* ssp. *brevifolius* Group A), Pose (*Poa secunda*), LeciW (*Leymus cinereus* wildland collections), LeciR (*Leymus cinereus* released varieties).

Species	Subpopulation				Species	Subpopulation			
	10%	30%	50%	70%		10%	30%	50%	70%
Brte v. Elmu	S	S	S	S	Elel v. Brte	S	S	S	S
Brte v. Pssp	S	S	S	NS	Elel v. Elmu	S	S	S	NS
Brte v. ElelC	S	S	S	NS	Elel v. Pssp	NS	S	S	S
Brte v. ElelB	S	S	S	S	Elel v. ElelC	NS	NS	NS	NS
Brte v. Elel	S	S	S	S	Elel v. ElelB	NS	NS	NS	NS
Brte v. ElelA	S	S	S	S	Elel v. ElelA	NS	NS	NS	NS
Brte v. Pose	S	S	S	S	Elel v. Pose	NS	NS	NS	NS
Brte v. LeciW	S	S	S	S	Elel v. LeciW	NS	NS	NS	NS
Brte v. LeciR	S	S	S	S	Elel v. LeciR	S	S	S	S
Elmu v. Brte	S	S	S	S	ElelA v. Brte	S	S	S	S
Elmu v. Pssp	NS	NS	NS	NS	ElelA v. Elmu	S	S	S	NS
Elmu v. ElelC	NS	S	NS	NS	ElelA v. Pssp	S	S	S	S
Elmu v. ElelB	NS	S	NS	NS	ElelA v. ElelC	NS	NS	NS	NS
Elmu v. Elel	S	S	S	NS	ElelA v. ElelB	NS	NS	NS	NS
Elmu v. ElelA	S	S	S	NS	ElelA v. Elel	NS	NS	NS	NS
Elmu v. Pose	S	S	S	S	ElelA v. Pose	NS	NS	NS	NS
Elmu v. LeciW	S	S	S	S	ElelA v. LeciW	NS	NS	NS	S
Elmu v. LeciR	S	S	S	S	ElelA v. LeciR	S	S	S	S

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Table 3. (continued)

Pssp v. Brte	S	S	S	NS	Pose v. Brte	S	S	S	S
Pssp v. Elmu	NS	NS	NS	NS	Pose v. Elmu	S	S	S	S
Pssp v. ElelC	NS	NS	NS	NS	Pose v. Pssp	S	S	S	S
Pssp v. ElelB	NS	NS	NS	NS	Pose v. ElelC	NS	NS	NS	S
Pssp v. Elel	NS	S	S	S	Pose v. ElelB	NS	NS	NS	NS
Pssp v. ElelA	S	S	S	S	Pose v. Elel	NS	NS	NS	NS
Pssp v. Pose	S	S	S	S	Pose v. ElelA	NS	NS	NS	NS
Pssp v. LeciW	NS	S	S	S	Pose v. LeciW	NS	NS	NS	NS
Pssp v. LeciR	S	S	S	S	Pose v. LeciR	NS	S	S	S
ElelC v. Brte	S	S	S	NS	LeciW v. Brte	S	S	S	S
ElelC v. Elmu	NS	S	NS	NS	LeciW v. Elmu	S	S	S	S
ElelC v. Pssp	NS	NS	NS	NS	LeciW v. Pssp	NS	S	S	S
ElelC v. ElelB	NS	NS	NS	NS	LeciW v. ElelC	NS	NS	S	S
ElelC v. Elel	NS	NS	NS	NS	LeciW v. ElelB	NS	NS	NS	NS
ElelC v. ElelA	NS	NS	NS	NS	LeciW v. Elel	NS	NS	NS	NS
ElelC v. Pose	NS	NS	NS	S	LeciW v. ElelA	NS	NS	NS	S
ElelC v. LeciW	NS	NS	S	S	LeciW v. Pose	NS	NS	NS	NS
ElelC v. LeciR	S	S	S	S	LeciW v. LeciR	NS	S	S	NS
ElelB v. Brte	S	S	S	S	LeciR v. Brte	S	S	S	S
ElelB v. Elmu	NS	S	NS	NS	LeciR v. Elmu	S	S	S	S
ElelB v. Pssp	NS	NS	NS	NS	LeciR v. Pssp	S	S	S	S
ElelB v. ElelC	NS	NS	NS	NS	LeciR v. ElelC	S	S	S	S
ElelB v. Elel	NS	NS	NS	NS	LeciR v. ElelB	S	S	S	S
ElelB v. ElelA	NS	NS	NS	NS	LeciR v. Elel	S	S	S	S
ElelB v. Pose	NS	NS	NS	NS	LeciR v. ElelA	S	S	S	S
ElelB v. LeciW	NS	NS	NS	NS	LeciR v. Pose	NS	S	S	S
ElelB v. LeciR	S	S	S	S	LeciR v. LeciW	NS	S	S	NS

Table 4. Significance matrix for individual comparisons of mean-germination-times for thermal accumulation as a function of planting date, water-potential range, seedlot-group pair, and selected subpopulations. Each seedlot-goup is arranged in order of relative germination-rate to facilitate general comparisons. Significant (S) and non-significant (NS) treatment comparisons were determined using the Fisher's protected least-square-difference test for significant main-treatment effects. Brte (*Bromus tectorum*), Elmu (*Elymus multisetus*), Pssp (*Pseudoroegneria spicata*), ElelC (*Elymus elymoides* ssp. *brevifolius* Group C), ElelB (*Elymus elymoides* ssp. *brevifolius* Group B), Elel (*Elymus elymoides* ssp. *elymoides*), ElelA (*Elymus elymoides* ssp. *brevifolius* Group A), Pose (*Poa secunda*), LeciW (*Leymus cinereus* wildland collections varieties), LeciR (*Leymus cinereus* released varieties).

| Species | 11-Dec | | | | 05-Mar | | | | 28-May | | | |
| | all | | >-1.0MPa | | all | | >-1.0MPa | | all | | >-1.0MPa | |
	10%	50%	10%	50%	10%	50%	10%	50%	10%	50%	10%	50%
Brte v. Elmu	S	NS	S	NS	S	NS	S	NS	S	NS	S	S
Brte v. Pssp	S	NS	S	NS	S	NS	S	S	S	S	S	S
Brte v. ElelC	S	S	S	S	S	S	S	S	S	S	S	S
Brte v. ElelB	S	NS	S	NS	S	S	S	S	S	S	S	S
Brte v. Elel	S	NS	S	NS	S	S	S	S	S	S	S	S
Brte v. ElelA	S	S	S	S	S	S	S	S	S	S	S	S
Brte v. Pose	S	S	S	S	S	S	S	S	S	S	S	S
Brte v. LeciW	S	S	S	S	S	S	S	S	S	S	S	S
Brte v. LeciR	S	S	S	S	S	S	S	S	S	-	S	-
Elmu v. Brte	S	NS	S	NS	S	NS	S	NS	S	NS	S	S
Elmu v. Pssp	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	S	NS
Elmu v. ElelC	S	S	S	S	S	S	NS	S	NS	NS	NS	NS
Elmu v. ElelB	S	S	NS	NS	S	NS	S	S	S	NS	S	S
Elmu v. Elel	S	S	S	NS	S	S	S	S	S	NS	S	S
Elmu v. ElelA	S	S	S	S	S	S	S	S	S	S	S	S
Elmu v. Pose	S	S	S	S	S	S	S	S	S	S	S	S
Elmu v. LeciW	S	S	S	S	S	S	S	S	S	S	S	S
Elmu v. LeciR	S	S	S	S	S	S	S	S	S	-	S	-

Table 4. (continued)

Pssp v. Brte	S	NS	S	NS	S	NS	S	S	S	S	S	S
Pssp v. Elmu	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	S	NS
Pssp v. ElelC	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Pssp v. ElelB	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Pssp v. Elel	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Pssp v. ElelA	S	S	S	S	S	S	S	S	S	S	S	S
Pssp v. Pose	NS	S	NS	S	S	S	S	S	S	S	S	S
Pssp v. LeciW	S	S	S	S	S	S	S	S	NS	S	S	S
Pssp v. LeciR	S	S	S	S	S	S	S	S	S	-	S	-
ElelC v. Brte	S	S	S	S	S	S	S	S	S	S	S	S
ElelC v. Elmu	S	S	S	S	S	S	NS	S	NS	NS	NS	NS
ElelC v. Pssp	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ElelC v. ElelB	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ElelC v. Elel	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ElelC v. ElelA	S	NS	S	NS	S	NS	S	NS	S	S	S	S
ElelC v. Pose	NS	NS	NS	NS	S	NS	S	NS	S	S	S	S
ElelC v. LeciW	NS	S	NS	S	S	S	S	S	NS	S	S	S
ElelC v. LeciR	S	S	S	S	S	S	S	S	S	-	S	-
ElelB v. Brte	S	NS	S	NS	S	S	S	S	S	S	S	S
ElelB v. Elmu	S	S	NS	NS	S	NS	S	S	S	NS	S	S
ElelB v. Pssp	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ElelB v. ElelC	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ElelB v. Elel	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ElelB v. ElelA	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ElelB v. Pose	NS	NS	NS	NS	NS	NS	NS	NS	NS	S	NS	NS
ElelB v. LeciW	NS	S	NS	S	NS	S	NS	S	NS	NS	NS	NS
ElelB v. LeciR	S	S	S	S	S	S	S	S	S	-	S	-

Table 4. (continued)

	1	2	3	4	5	6	7	8	9	10	11	12
Elel v. Brte	S	NS	S	NS	S	S	S	S	S	S	S	S
Elel v. Elmu	S	S	S	NS	S	S	S	S	S	NS	S	S
Elel v. Pssp	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Elel v. ElelC	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Elel v. ElelB	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Elel v. ElelA	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Elel v. Pose	NS	NS	NS	NS	NS	NS	NS	NS	S	S	NS	S
Elel v. LeciW	NS	S	NS	S	NS	S	NS	S	NS	S	NS	S
Elel v. LeciR	S	S	S	S	S	S	S	S	S	-	S	-
ElelA v. Brte	S	S	S	S	S	S	S	S	S	S	S	S
ElelA v. Elmu	S	S	S	S	S	S	S	S	S	S	S	S
ElelA v. Pssp	S	S	S	S	S	S	S	S	S	S	S	S
ElelA v. ElelC	S	NS	S	NS	S	NS	S	NS	S	S	S	S
ElelA v. ElelB	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ElelA v. Elel	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
ElelA v. Pose	NS	NS	NS	NS	NS	NS	NS	NS	NS	S	NS	NS
ElelA v. LeciW	NS	S	NS	S	NS	S	NS	S	NS	NS	NS	S
ElelA v. LeciR	S	S	S	S	S	S	S	S	S	-	S	-
Pose v. Brte	S	S	S	S	S	S	S	S	S	S	S	S
Pose v. Elmu	S	S	S	S	S	S	S	S	S	S	S	S
Pose v. Pssp	NS	S	NS	S	S	S	S	S	S	S	S	S
Pose v. ElelC	NS	NS	NS	NS	S	NS	S	NS	S	S	S	S
Pose v. ElelB	NS	NS	NS	NS	NS	NS	NS	NS	NS	S	NS	NS
Pose v. Elel	NS	NS	NS	NS	NS	NS	NS	NS	S	S	NS	S
Pose v. ElelA	NS	NS	NS	NS	NS	NS	NS	NS	NS	S	NS	NS
Pose v. LeciW	NS	NS	NS	S	NS	NS	NS	S	NS	NS	NS	NS
Pose v. LeciR	S	S	S	S	S	S	S	S	S	-	S	-

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Table 4. (continued)

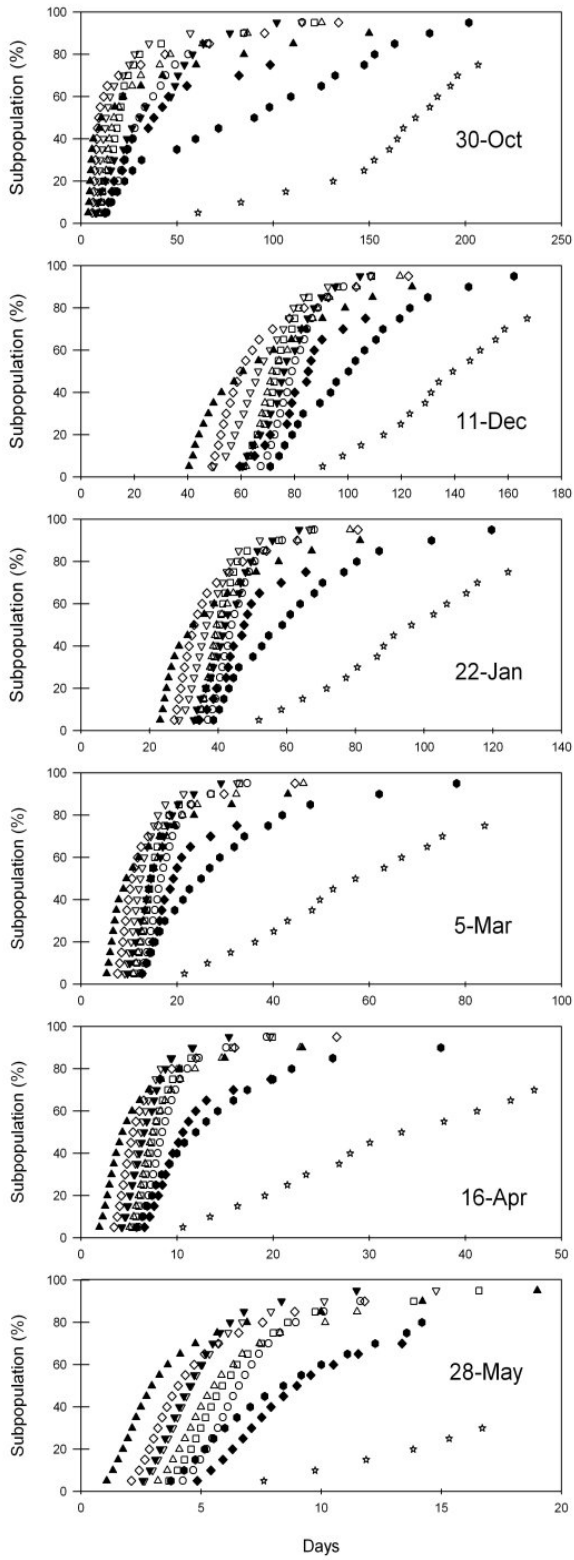|	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12
LeciW v. Brte	S	S	S	S	S	S	S	S	S	S	S	S
LeciW v. Elmu	S	S	S	S	S	S	S	S	S	S	S	S
LeciW v. Pssp	S	S	S	S	S	S	S	S	NS	S	S	S
LeciW v. ElelC	NS	S	NS	S	S	S	S	S	NS	S	S	S
LeciW v. ElelB	NS	S	NS	S	NS	S	NS	S	NS	NS	NS	NS
LeciW v. Elel	NS	S	NS	S	NS	S	NS	S	NS	S	NS	S
LeciW v. ElelA	NS	S	NS	S	NS	S	NS	S	NS	NS	NS	S
LeciW v. Pose	NS	NS	NS	S	NS	NS	NS	S	NS	NS	NS	NS
LeciW v. LeciR	S	S	S	S	S	S	S	S	S	-	S	-
LeciR v. Brte	S	S	S	S	S	S	S	S	S	-	S	-
LeciR v. Elmu	S	S	S	S	S	S	S	S	S	-	S	-
LeciR v. Pssp	S	S	S	S	S	S	S	S	S	-	S	-
LeciR v. ElelC	S	S	S	S	S	S	S	S	S	-	S	-
LeciR v. ElelB	S	S	S	S	S	S	S	S	S	-	S	-
LeciR v. Elel	S	S	S	S	S	S	S	S	S	-	S	-
LeciR v. ElelA	S	S	S	S	S	S	S	S	S	-	S	-
LeciR v. Pose	S	S	S	S	S	S	S	S	S	-	S	-
LeciR v. LeciW	S	S	S	S	S	S	S	S	S	-	S	-
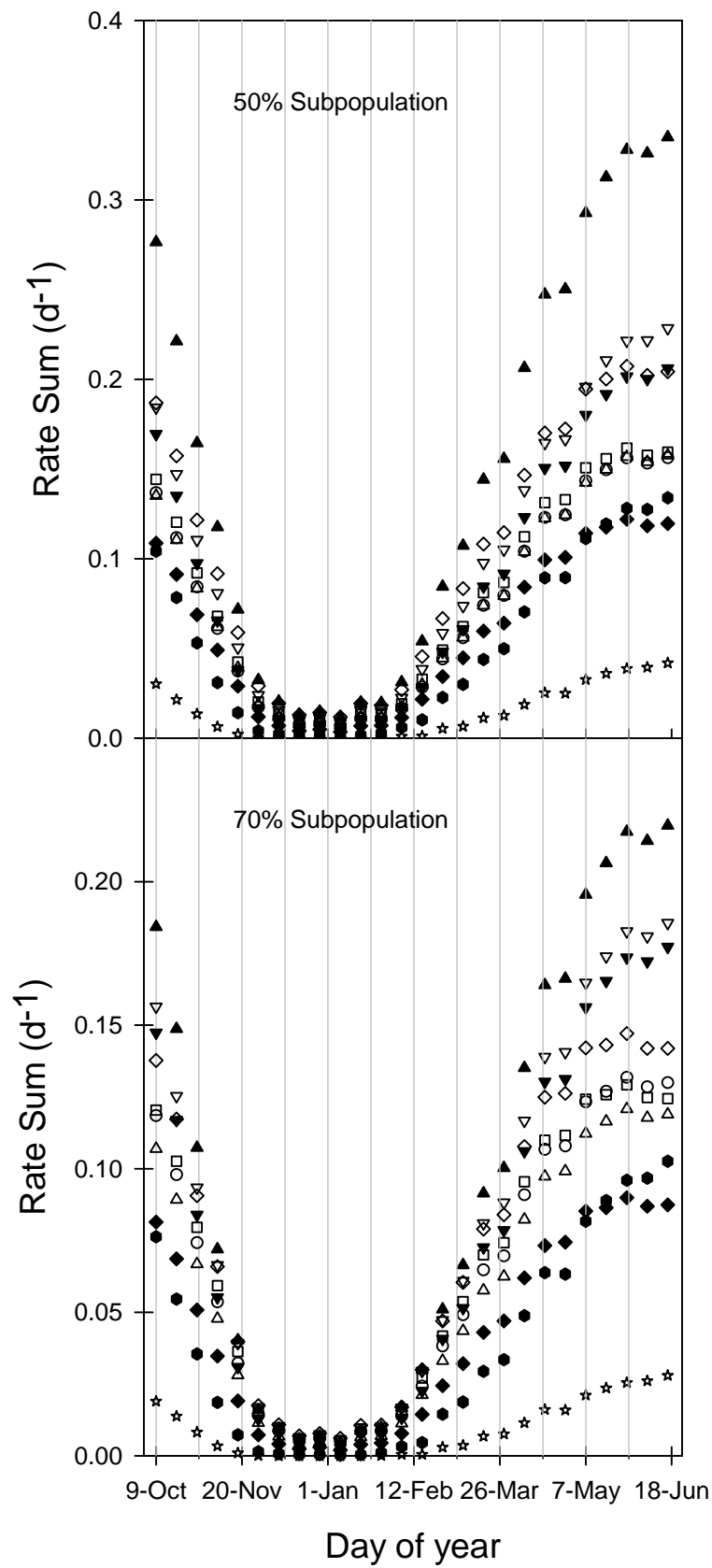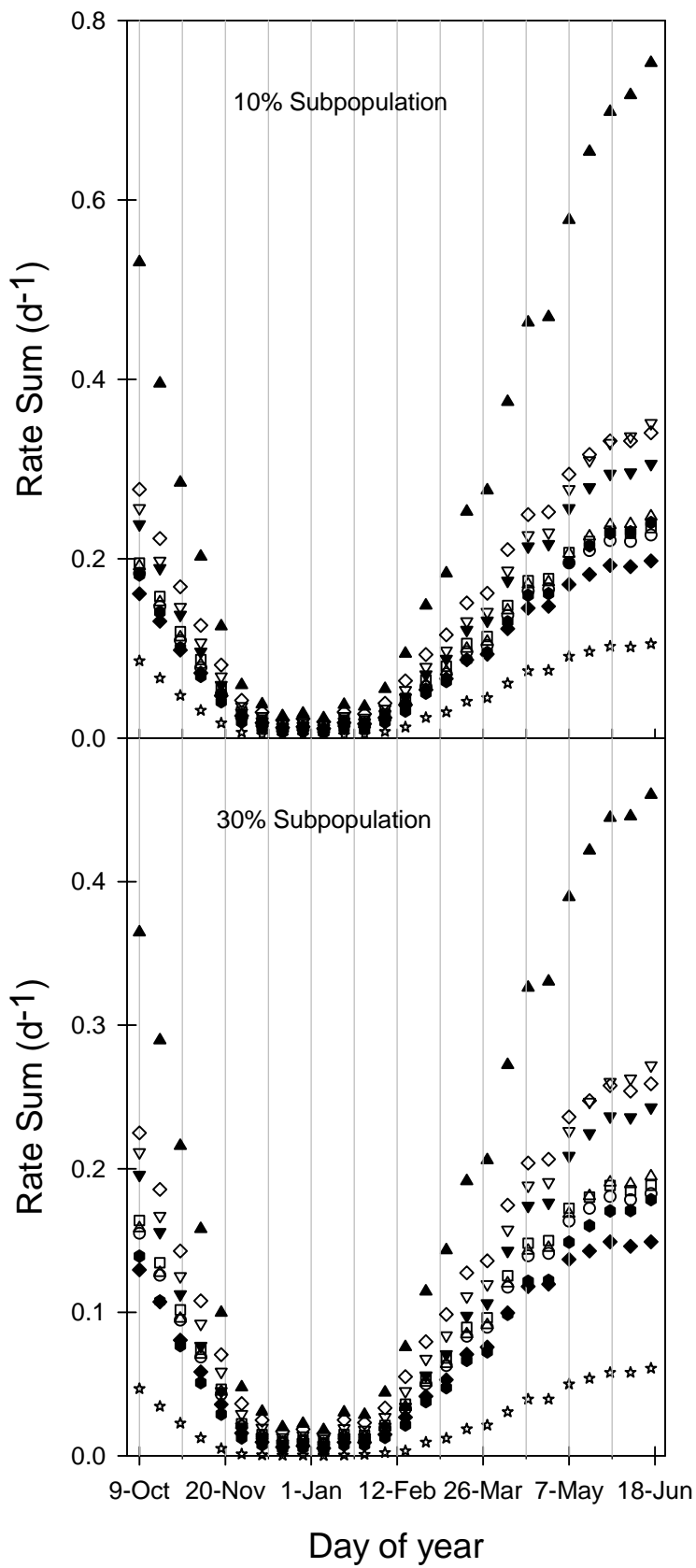
Fig. 1
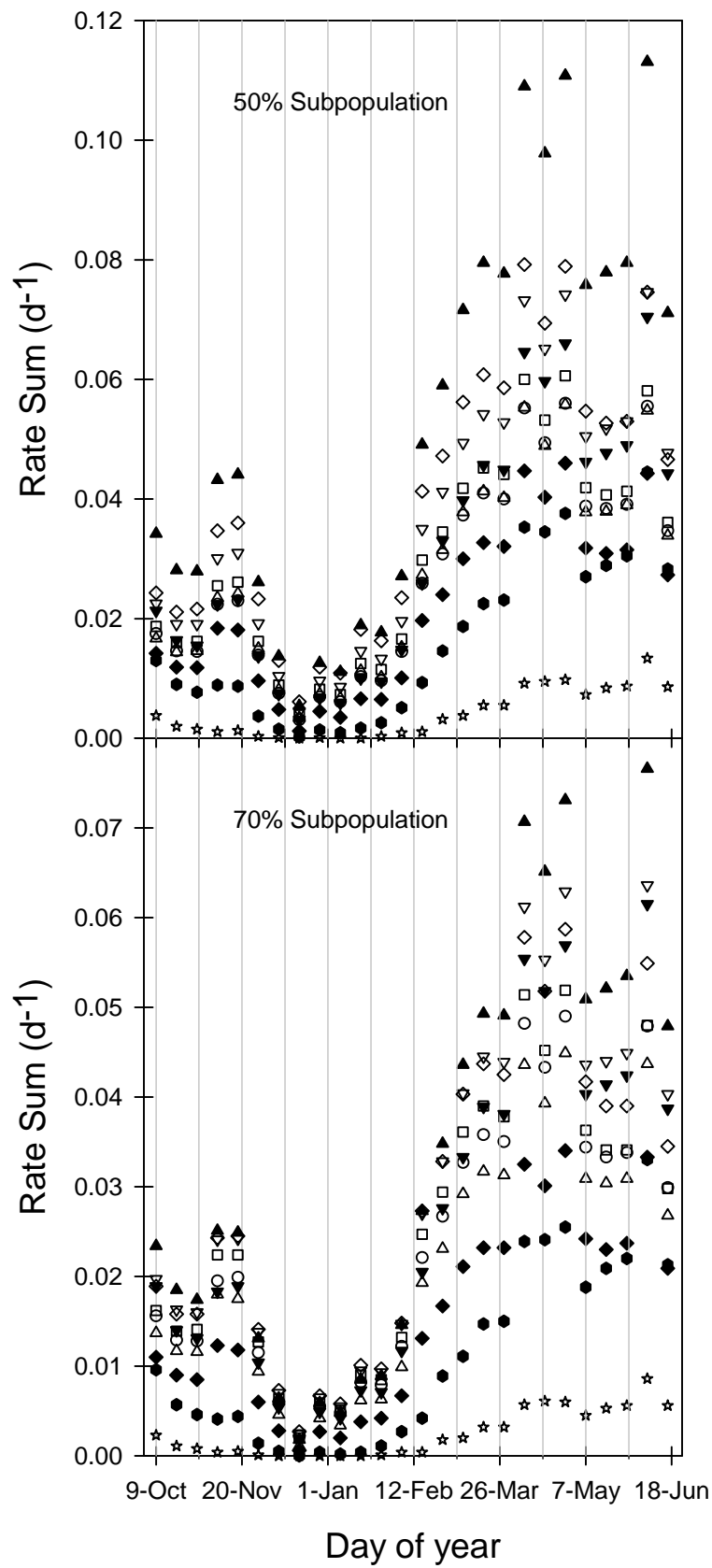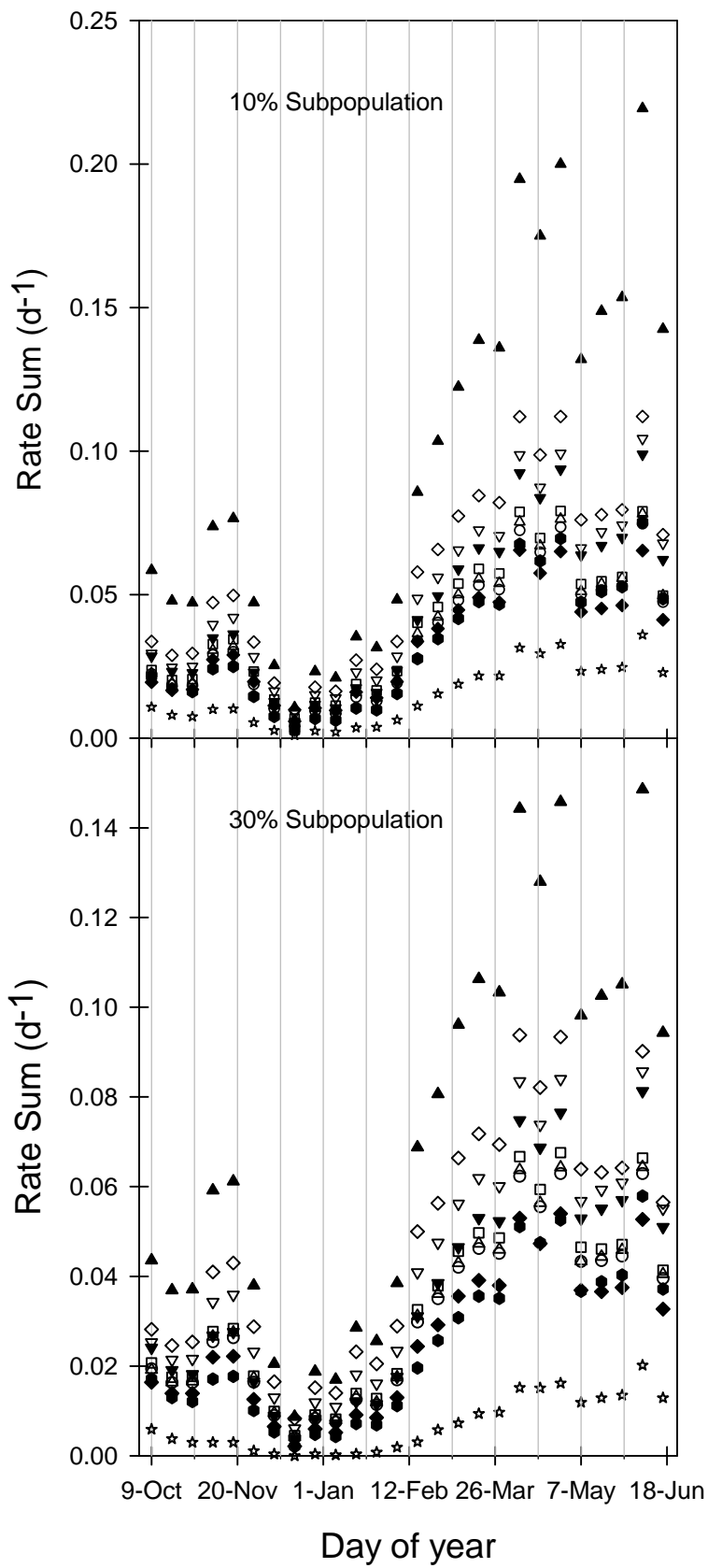
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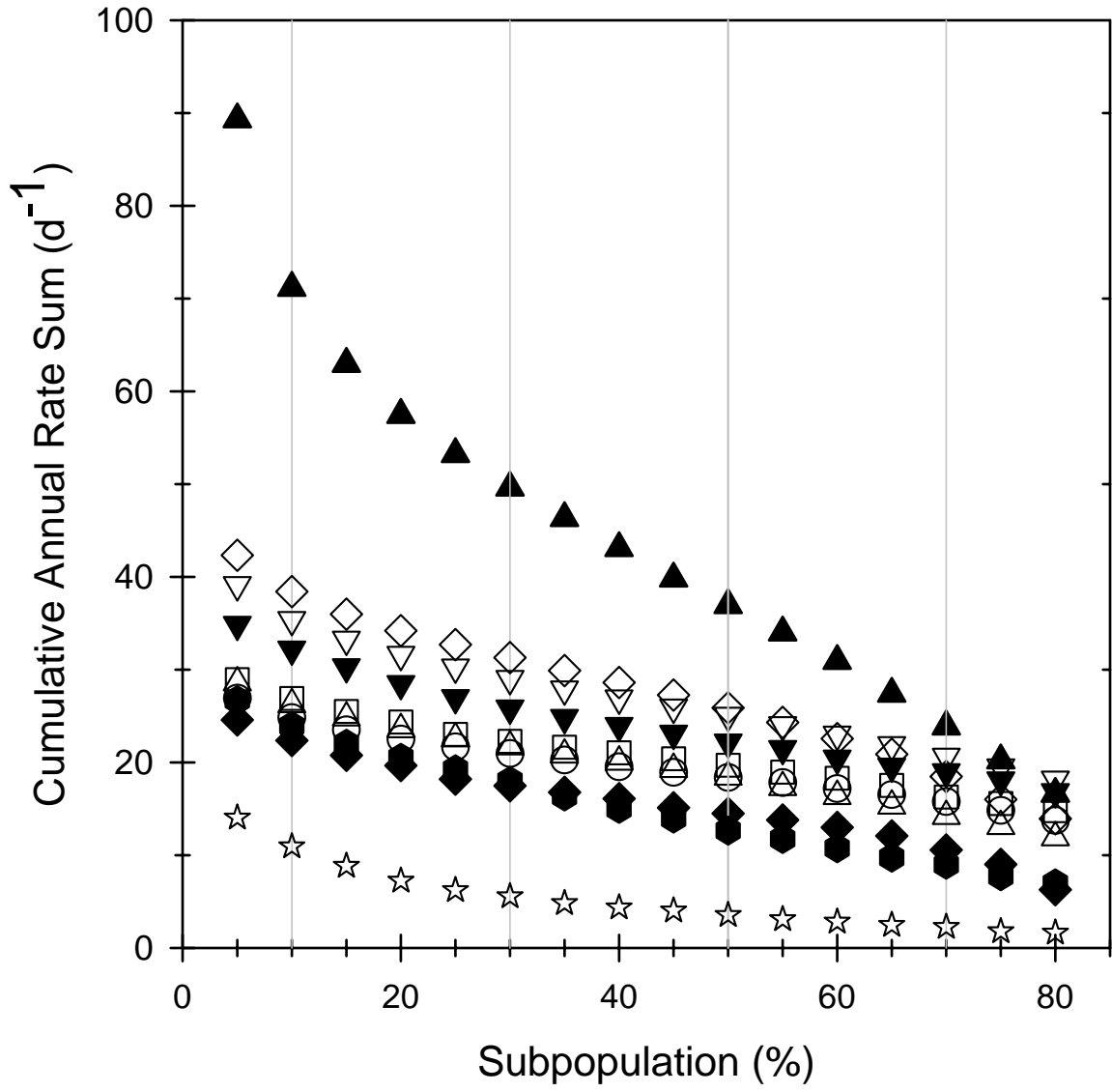
Fig.3

A. Thermal Accumulation All Temperatures

B. Thermal Accumulation above -1.0 MPa

30-Oct

11-Dec

22-Jan

5-Mar

16-Apr

28-May

Fig. 4