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Use of degree-days in multiple-temperature experiments

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Abstract

This research compared results from germination and growth when the experiment duration was chronologically set or based on degree-days. Seeds of smooth brome (*Bromus inermis* Leyss.), plains rough fescue (*Festuca altaica* Trin. subsp. *hallii* (Vasey) Harms), prairie coneflower (*Ratibida columnifera* (Nutt.) Woot. and Standl.), and silver sagebrush (*Artemisia cana* Pursh.) were germinated at 5, 10, 15, 20, and 25°C for 28 days or 400 degree-days (Base temperature = 0°C). Root and shoot weights of seedlings of these species were compared at 5, 10, 15, 20, 25 and 30°C after growing them 20 days or 200 degree-days. With the exception of prairie coneflower, optimal temperatures for germination were 2 to 4°C lower when incubated 400 degree-days compared to 28 days. Total germination for prairie coneflower was not significantly different (P =0.454) at 28 days or 400 degree-days. Interacting effects of the duration of experiments and temperature significantly ($P \leq 0.001$) influenced root and shoot weight of all species. Except for shoot weight of smooth brome, predicted optimum temperatures for root and shoot growth were 7 to 21°C lower at 200 degree-days than 20 days. These experiments illustrate that results from germination and growth studies can vary substantially depending on whether chronological time or degree-days are used as the end point. Thus, ecological interpretations or management recommendations can be quite different. Degree-days may be more meaningful than chronological units for germination and growth studies because they integrate time and temperature. The use of degree-days as an end point for experiments rather than chronological time deserves further consideration by researchers.

Key Words: *Artemisia cana*, *Bromus inermis*, *Festuca altaica* subsp. *hallii*, germination, *Ratibida columnifera*, root growth, shoot growth, thermal units

Researchers have long been interested in studying germination and plant responses to temperature. Comparisons are often made between temperatures after incubating seeds or growing plants in controlled conditions for set periods of time. Results from these studies are then used to make ecological interpretations or management prescriptions. However, because plant processes are temperature dependent (Johnson and Thornley 1985), erroneous conclusions may be drawn if time is used as the independent variable at various temperatures. Generally as temperatures rise, plant processes increase to a maximum, declining above some optimum (Grace 1988). When results from experiments at different temperatures are compared, arbitrarily set chronological time limits introduce time as a confounding factor because equal thermal units do not accumulate at each temperature.

Degree-days or thermal units have been successfully utilized to describe or predict insect phenology (Dennis et al. 1986, Dennis and Kemp 1988), bud burst in trees (Thomson and Moncrieff 1982, Hunter and Lechowicz 1992), pollen shedding (Boyer 1973), flowering in several range plants (White 1979), anthesis and maturity of wheat (*Triticum aestivum* L.) and corn (*Zea mays* L.) (Gilmore and Rodgers 1958, Cross and Zuber 1972, Davidson and Campbell 1983, Bauer et al. 1984), growth of forage species (Holt and Haferkamp 1987, Frank and Hofmann 1989, Frank 1991, Gillen and Ewing 1992, Harrison and Romo 1994) and germination and emergence of several species (Carberry and Campbell 1989, Jordan and Haferkamp 1989). Degree-days have, however, received limited use as time limits where results are compared from experiments conducted at different temperatures. The purpose of the research reported here was to test whether interpretation of data from germination and growth studies at several temperatures would be significantly different if the duration of experiments is chronologically set or based on degree-days.

Materials and Methods

In 1987 seeds of plains rough fescue (*Festuca altaica* subsp. *hallii* (Vasey) Harms) and smooth brome (*Bromus inermis* Leyss.) were collected at the University of Saskatchewan's Kernen Prairie (Pylypec 1986), 1 km east of Saskatoon. Prairie coneflower (*Ratibida columnifera* (Nutt.) Woot. and Standl.) and silver sagebrush (*Artemisia cana* Pursh.) were collected at the University of Saskatchewan's Matador Research Station (Coupland et al. 1974), approximately 70 km north of Swift Current, Saskatchewan. The native species were selected because their seeds were readily available, they were different life forms,

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and they were from different habitats. Smooth brome was chosen because it is a naturalized exotic that has been subject to intense selection pressure by forage breeders. About 2 weeks after collection seeds were cleaned with hand-held sieves and stored in paper envelopes in darkness in the laboratory.

Germination Experiments

In germination experiments, durations of 28 days and 400 degree-days, and temperatures of 5, 10, 15, 20, or 25°C were factorially applied in a randomized complete block design with 4 replicates of 50 seeds for each species. Daily incubation temperatures were used to calculate accumulated degree-days using a base temperature of 0°C (Eq. 1).

$$\text{Accumulated degree-days} = \sum [(\text{Daily temperature°C} - \text{Base temperature°C})/2] \quad (1)$$

The seeds were placed in closed petri dishes on 1-mm thick germination paper that was moistened with distilled water and incubated in darkness. Germination was checked weekly and germinated seeds were removed; distilled water was added to the petri dishes to keep the seeds moist. During the germination checks seeds were briefly exposed to light. Seeds of the grasses were considered germinated when the radicle and plumule were both ≥5-mm long whereas silver sagebrush and prairie coneflower were counted if the cotyledons were reflexed and the radicle was ≥5-mm long.

Total germination data for each species were analyzed with factorial analysis of variance (Petersen 1985) after transforming the percentages with arcsin $\sqrt{p}$ (Snedecor and Cochran 1980). When the temperature-by-duration interaction was significant ($P \leq 0.05$), data from the 2 experiments were separated and the best-fit regression equations (Petersen 1985) were determined after the data were back-transformed. If the interaction was not significant ($P \leq 0.05$), the significance of the duration of the experiment and temperature was considered and the best-fit ($P \leq 0.05$) regression equation was calculated.

Seedling Growth

In the seedling growth experiments durations of 20 days and 200 degree-days (Eq. 1) (Base temperature = 0°C) and temperatures of 5, 10, 15, 20, 25, or 30°C were factorially applied in a randomized complete block design with 4 replicates. Seeds of each species were incubated in darkness at 20°C in petri dishes that were prepared as described above. Seedlings at 2 days of age were individually transplanted to pots containing premoistened "Redi-earth" potting medium. These plants were grown in growth chambers and watered at 2-day intervals. All growth chambers provided a 12 hour photoperiod standardized at 395 μmol m^{-2} s^{-1}. At 20 days or 200 degree-days, plants of each species were removed from the pots, and the potting medium was carefully removed from the roots by washing in water. The roots were separated from the shoots, and both were dried at 60°C for 48 hours and weighed.

Root and shoot weights for each species were analyzed with factorial analysis of variance (Petersen 1985). When the temperature-by-duration interaction was significant ($P \leq 0.05$), data from the 2 experiments were separated and the best-fit regression equations ($P \leq 0.05$) were determined over the temperature range (Petersen 1985).

Results

Germination Experiment

With the exception of prairie coneflower, the duration-by-temperature interaction significantly ($P \leq 0.001$) influenced total germination (Table 1). This highly significant interaction indicates that temperature influenced germination uniquely depending on whether the length of the experiment was chronologically set or based on degree-days. The non-significant ($P = 0.454$) temperature-by-duration interaction for prairie coneflower indicates that the criterion for terminating experiments was not important.

When data from the 2 experiments were combined in regression analyses, the predicted optimum temperature for germination of prairie coneflower was 15°C (Table 2, Fig. 1). Separate regression equations were developed for the 2 experiments for plains rough fescue, silver sagebrush, and smooth brome. For germination of silver sagebrush the predicted optimum was 12°C at 28 days and 8°C at 400 degree-days (Table 2, Fig. 2). The predicted optimum for germination of plains rough fescue was 16°C at 28 days and 12°C at 400 degree-days (Table 2, Fig. 3). Optimum temperatures for smooth brome germination were 18°C at 28 days and 16°C at 400 degree-days (Table 2, Fig. 4). Germination of the later 3 species was higher at lower temperatures at 400 degree-days than at 28 days.

Table 1. Analyses of variance for total germination of seeds incubated at constant temperatures of 5, 10, 15, 20, or 25°C for 28 days or 400 degree-days (Base temperature = 0°C).

Source	D.F.	Mean Square	F	P
		Smooth brome		
Replicate (R)	3	58	1.2	0.342
Temperature (T)	4	2566	51.3	<0.001
Duration (D)	1	270	5.4	0.028
D x T	4	476	9.5	<0.001
Error	27	50		
		Silver sagebrush		
R	3	43	1.0	0.396
T	4	2736	65.8	<0.001
D	1	84	2.0	0.166
D x T	4	170	4.1	0.010
Error	27	42		
		Prairie coneflower		
R	3	21	0.3	0.826
T	4	4990	72.1	<0.001
D	1	40	0.6	0.454
D x T	4	147	2.1	0.105
Error	27	69		
		Plains rough fescue		
R	3	67	1.3	0.308
T	4	4412	82.7	<0.001
D	1	1082	20.3	<0.001
D x T	4	1512	28.3	<0.001
Error	27	53		

Seedling Growth Experiment

The interaction of duration-by-temperature significantly ($P \leq 0.001$) influenced root and shoot weight of all species (Table 3). Therefore separate regression equations were developed for each species in the

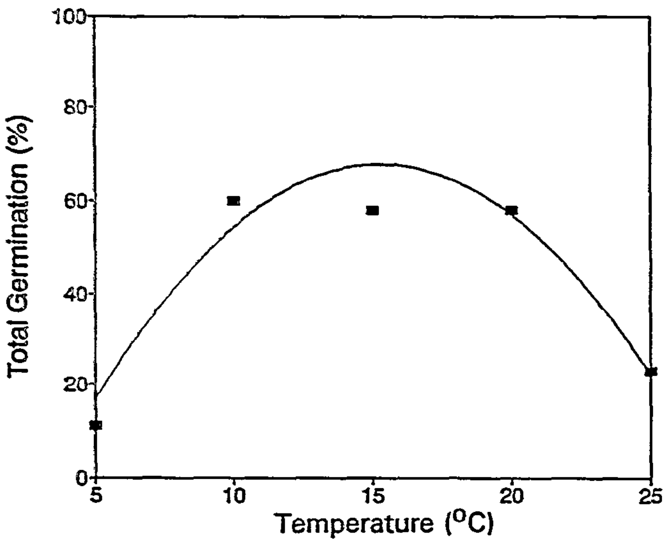

Fig. 1. Response curve for total germination of prairie coneflower incubated at 5, 10, 15, 20, or 25°C for 28 days or 400 degree-days. Each symbol is the mean of 8 replicates. The regression equation is presented in Table 2.

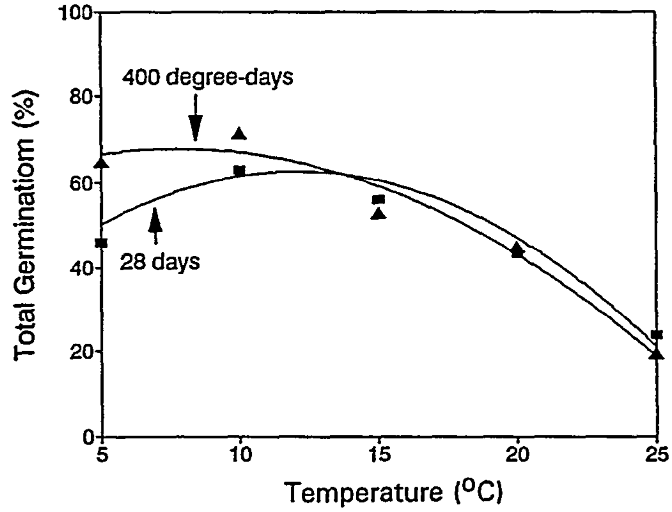

Fig. 2. Response curves for total germination of silver sagebrush incubated at 5, 10, 15, 20, or 25°C for 28 days (■) or 400 degree-days (▲). Each symbol is the mean of 4 replicates. Regression equations are presented in Table 2.

2 experiments. With the exception of shoot weight of smooth brome, predicted optimum temperatures were greater at 20 days than at 200 degree-days.

When grown for 20 days the predicted optimum temperature for shoot and root biomass of prairie coneflower was ≥30°C (Table 2, Fig. 5). In sharp contrast, the predicted optimum temperatures for shoot and root biomass were 17 and 15°C, respectively, at 200 degree-days.

When silver sagebrush was grown for 20 days the predicted optimum for shoot biomass was 22°C (Table 3, Fig. 6); shoot weight did not differ over the 5–30°C range at 200 degree-days. Root growth increased from 5 to 21°C during the 20 day growth

Table 2. Regression equations for total germination, root and shoot biomass for 4 species. X is temperature (°C).

Species	Experiment Duration	Regression Equation	R^2	P
		Total Germination (%)		
Prairie	28 days	$Y=-45.2+14.8X-0.484X^2$	0.74	<0.001
coneflower	400 degree-days[1]	—[2]	—	—
Silver	28 days	$Y=26.3+6.0X-0.249X^2$	0.77	<0.001
sagebrush	400 degree-days	$Y=57.8+2.6X-0.166X^2$	0.90	<0.001
Plains rough	28 days	$Y=-71.6+19.2X-0.603X^2$	0.78	<0.001
fescue	400 degree-days	$Y=34.4+7.2X-0.296X^2$	0.79	<0.001
Smooth	28 days	$Y=-28.7+13.9X-0.396X^2$	0.94	<0.001
brome	400 degree-days	$Y=27.2+7.59-0.237X^2$	0.62	<0.001
		Shoot biomass (g plant^{-1})		
Prairie	20 days	$Y=-1.060+0.242X-0.002X^2$	0.83	<0.001
coneflower	200 degree-days	$Y=0.410+0.095X-0.003X^2$	0.31	0.021
Silver	20 days	$Y=-2.080+0.488X-0.011X^2$	0.60	<0.001
sagebrush	200 degree-days	N.S.[3]	—	0.257
Plains rough	20 days	$Y=-0.155+0.138X-0.003X^2$	0.63	<0.001
fescue	200 degree-days	$Y=0.347+0.077X-0.003X^2$	0.50	0.001
Smooth	20 days	$Y=-10.90+2.190X-0.043X^2$	0.74	<0.001
brome	200 degree-days	$Y=3.79-0.057X$	0.22	0.022
		Root biomass (g plant^{-1})		
Prairie	20 days	$Y=-0.837+0.186X-0.003X^2$	0.78	<0.001
coneflower	200 degree-days	$Y=0.085+0.068X-0.002X^2$	0.52	<0.001
Silver	20 days	$Y=-0.320+0.103X-0.002X^2$	0.49	0.001
sagebrush	200 degree-days	$Y=0.477-0.013X$	0.63	<0.001
Plains rough	20 days	$Y=-0.033+0.040X$	0.72	<0.001
fescue	200 degree-days	$Y=0.163+0.029X-0.001X^2$	0.25	0.047
Smooth	20 days	$Y=2.12-0.046X$	0.44	<0.001
brome	200 degree-days	$Y=-5.05+1.05X-0.022X^2$	0.58	<0.001

[1] Base temperature = 0°C.
[2] Total germination at 28 days and 400 degree-days was not significantly different (See Table 1). Data from both experiments were pooled for regression analysis.
[3] Regression equation not significant at $P\leq0.05$.

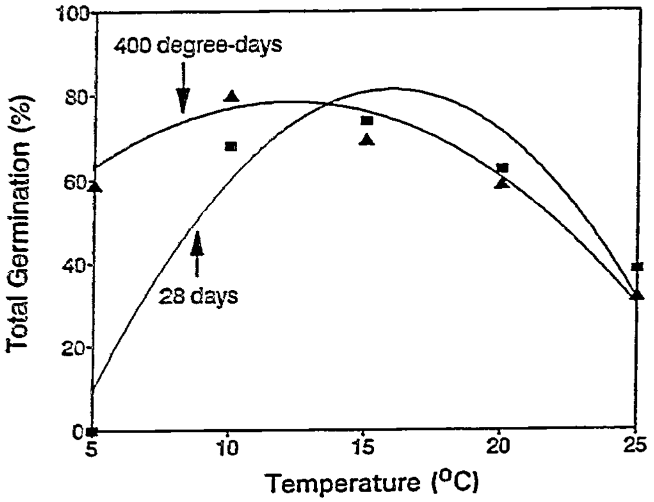

Fig. 3. Response curves for total germination of plains rough fescue incubated at 5, 10, 15, 20, or 25°C for 28 days (■) or 400 degree-days (▲). Each symbol is the mean of 4 replicates. Regression equations are presented in Table 2.

period; however, over the 5–30°C range root biomass decreased linearly when grown 200 degree-days.

The predicted optimum temperature for shoot growth of plains rough fescue was 22°C at 20 days and 15°C at 200 degree-days (Table 2, Fig. 7). Root weight of plains rough fescue increased linearly from 5–30°C when grown for 20 days, but the predicted optimum was 16°C when seedlings were grown 200 degree-days.

The predicted optimum temperatures for shoot biomass of smooth brome were 26°C and 5°C when grown 20 days and 200 degree-days, respectively (Table 3, Fig. 8). Root weight declined linearly over the 5–30°C range when seedlings were grown for

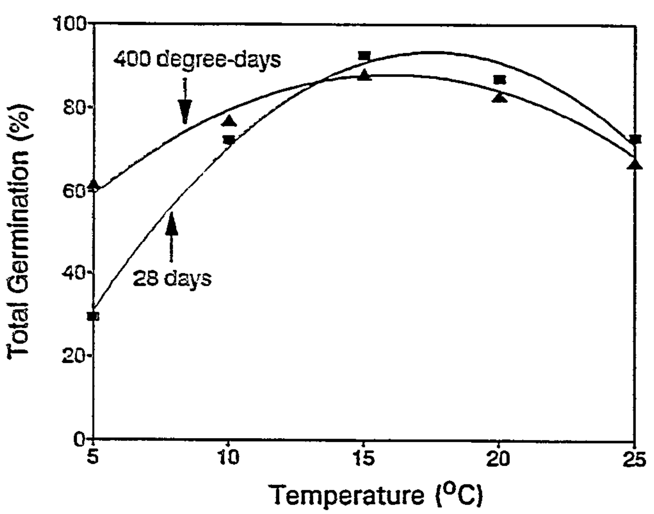

Fig. 4. Response curves for total germination of smooth brome incubated at 5, 10, 15, 20, 25, or 30°C for 28 days (■) or 400 degree-days (▲). Each symbol is the mean of 4 replicates. Regression equations are presented in Table 2.

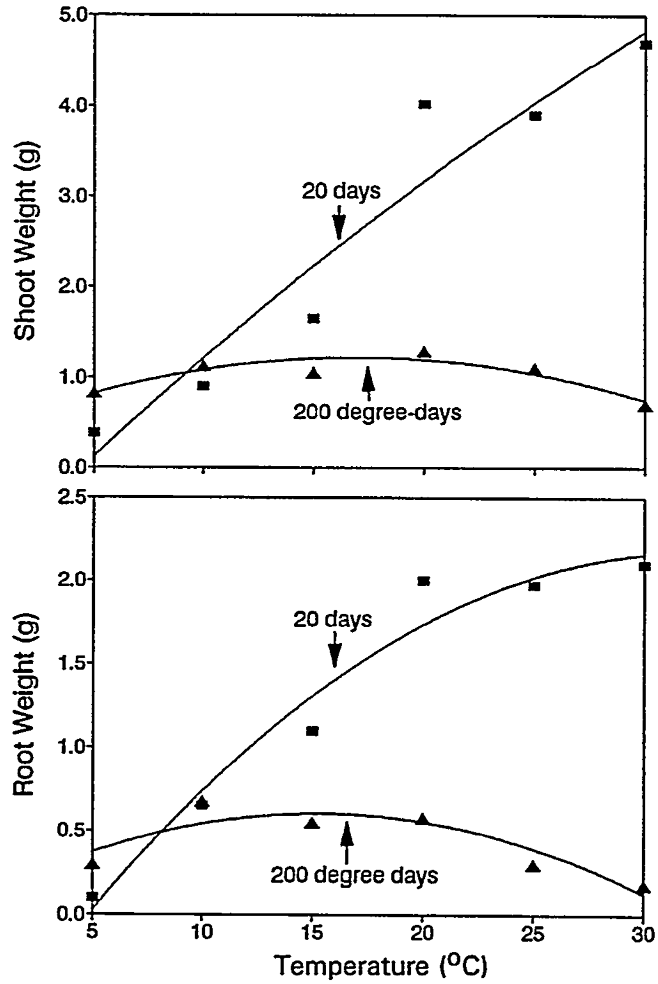

Fig. 5. Response curves for root and shoot growth of prairie coneflower seedlings grown at 5, 10, 15, 20, 25, or 30°C for 20 days (■) or 200 degree-days (▲). Each symbol is the mean of 4 replicates. Regression equations are presented in Table 2.

200 degree-days, but the optimum temperature was 24°C at 20 degree-days.

Discussion

Experiments where chronological time limits have been used have provided useful information for ecological interpretations and management. Utilizing chronological limits provides (1) comparisons with previously published data from studies of similar length, (2) short completion time for experiments, and (3) low costs of research. By contrast a disadvantage of using degree-days is that the period of experimentation may be increased and costs may also rise. For example in the present study 80 days were required at 5°C to accumulate 400 degree-days, but only 13.3 days were required at 30°C.

How species respond to temperatures after exposure to certain temperatures for chronologically set periods of time are also easi-

Table 3. Analyses of variance for root and shoot weight for seedlings grown at 5, 10, 15, 20, 25 and 30°C for 20 days or 200 degree-days (Base temperature = 0°C).

Source	D.F.	Mean Square (Root Weight (g))	F	P	Mean Square (Shoot Weight (g))	F	P
Smooth brome							
Replicate (R)	3	3.8	1.6	0.216	3.3	0.8	0.510
Temperature (T)	5	17.6	7.2	<0.001	109.7	26.1	<0.001
Duration (D)	1	157.3	64.5	<0.001	826.7	197.0	<0.001
D x T	5	26.1	10.7	<0.001	132.3	31.5	<0.001
Error	33	2.4			4.2		
Silver sagebrush							
R	3	0.086	3.4	0.029	0.679	1.8	0.174
T	5	0.082	3.2	0.018	3.546	9.2	<0.001
D	1	1.203	47.7	<0.001	24.797	64.2	<0.001
D x T	5	0.296	11.7	<0.001	3.703	9.6	<0.001
Error	33	0.025			0.386		
Prairie coneflower							
R	3	0.034	0.3	0.813	0.267	1.1	0.365
T	5	1.298	89.2	<0.001	6.856	28.1	<0.001
D	1	9.541	12.1	<0.001	29.925	122.6	<0.001
D x T	5	1.646	15.4	<0.001	6.821	27.9	<0.001
Error	33	0.107			0.244		
Plains rough fescue							
R	3	0.083	3.3	0.033	0.016	0.3	0.794
T	5	0.284	11.3	<0.001	0.559	10.0	<0.001
D	1	1.435	56.8	<0.001	1.725	30.9	<0.001
D x T	5	0.362	14.3	<0.001	0.217	3.9	0.007
Error	33	0.025			0.056		

ly determined. If the duration of chronologically set experiments is sufficient for maximum germination at the lowest temperatures tested, there is no advantage of using degree-days and interpretation of results will not differ between the 2 techniques.

The use of degree-days becomes important when there is not a sufficient amount of germination at the low temperature using the chronologically set time period. Two parameters must be determined to use the degree-days approach: (1) the base temperature, and (2) the required number of degree-days. Base temperatures can be determined by regressing germination or growth on temperature (Arnold 1959), or if base temperatures are not known, 0°C can be used (e.g. Bauer et al. 1984, Frank and Hoffmann 1989, Gillen and Ewing 1992, Romo et al. 1991, Grilz et al. 1994). Caution must be exercised when comparing species, genotypes, and different stages of growth for they have different base temperature thresholds (Wang 1960). If the base temperature is changed, appropriate adjustments in the length of study will be required at each temperature, but relationships between temperatures will not change. Similarly if higher or lower temperatures are included in the experiments, the length of study will need to be lengthened or shortened. The number of degree-days chosen for the length of experimentation is subject to the objectives of each study. It is most meaningful to set degree-day limits that are biologically meaningful and correspond with field conditions and the stages of growth being studied.

The degree-days concept assumes that development is linearly related to temperature between the base temperature and the optimum temperature (Sharpe and DeMichele 1977). In addition it is assumed a certain stage of development is achieved when a specific number of degree days have accumulated above the base temperature (Hunter and Lechowicz 1992). Thus, when germination and growth experiments are conducted for chronologically set time, it should not be unexpected to find temperature limitations as temperatures decline from the optimum. As a result, ecological interpretations or management recommendations can deviate considerably. For example, in the present study predicted temperatures for germination and growth from the experiments with chronologically set time limits would be warmer than those determined when degree-days were used.

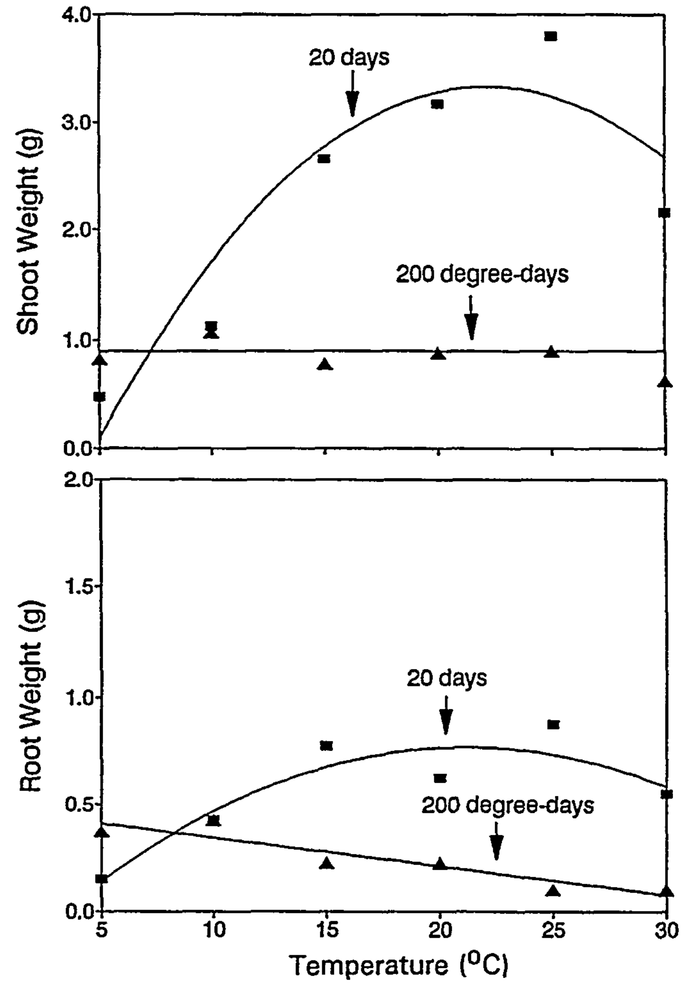

Fig. 6. Response curves for root and shoot growth of silver sagebrush seedlings grown at 5, 10, 15, 20, 25, or 30°C for 20 days (■) or 200 degree-days (▲). Each symbol is the mean of 4 replicates. Regression equations are presented in Table 2.

Although constant temperatures were used in the present studies, the use of degree-days is not restricted to them. If alternating temperatures are chosen, degree-days can be calculated (Eq. 2).

$$\text{Accumulated degree-days} = \sum [(\text{Maximum temperature°C} + \text{Minimum temperature°C} - \text{Base temperature°C})/2] \qquad (2)$$

For example, emergence and growth of wild oat (*Avena fatua* L.) under several alternating temperature regimes were compared after standardizing with degree-days (Rooney et al. 1989). Romo et al. (1991) and Grilz et al. (1994) also used cumulative degree-days to determine the effects of increasing or decreasing tempera-

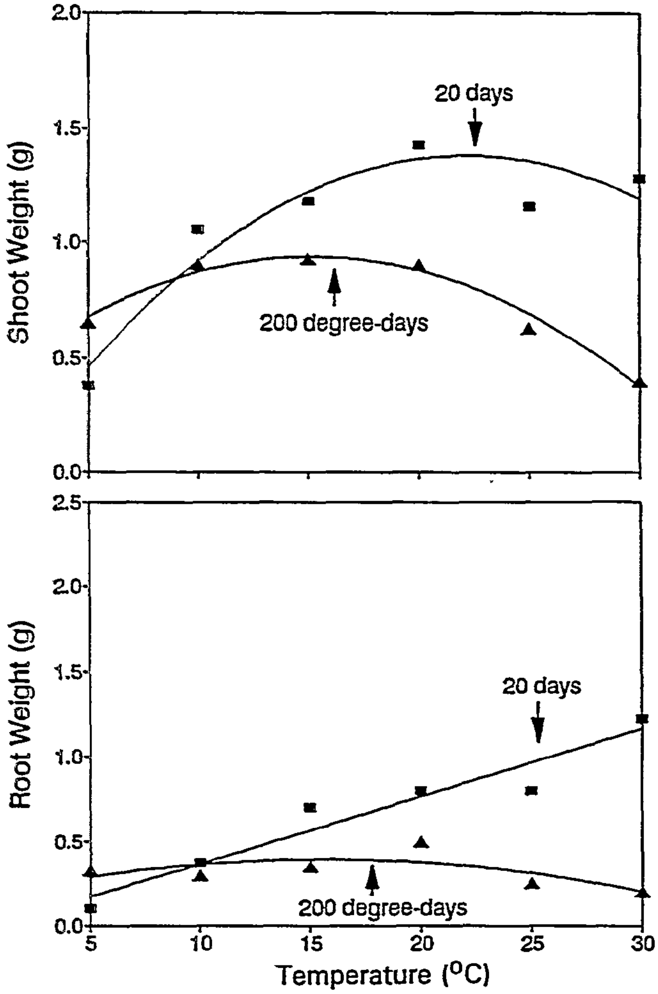

Fig. 7. Response curves for root and shoot growth of plains rough fescue seedlings grown at 5, 10, 15, 20, 25, or 30°C for 20 days (■) or 200 degree-days (▲). Each symbol is the mean of 4 replicates. Regression equations are presented in Table 2.

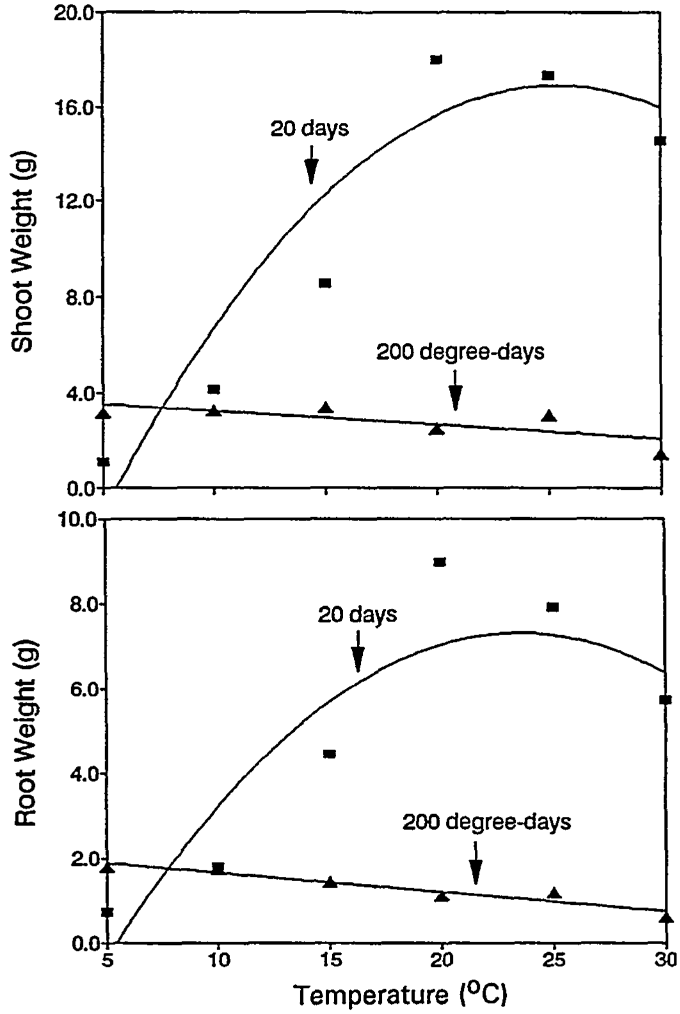

Fig. 8. Response curves for root and shoot growth of smooth brome seedlings grown at 5, 10, 15, 20, 25, or 30°C for 20 days (■) or 200 degree-days (▲). Each symbol is the mean of 4 replicates. Regression equations are presented in Table 2.

tures on germination of plains rough fescue and smooth brome, studies that would not have been possible without using degree-days.

Degree-days are biologically more meaningful than chronological units because they integrate time and temperature (Johnson and Thornley 1985). Therefore degree-days reduce artificially introduced effects of time when results are compared from experiments that are conducted at different temperatures. Use of degree-days may also improve predictions of field performance from studies conducted under controlled environmental conditions. The applicability of degree-days in multiple-temperature germination and growth studies merits additional consideration and research.

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