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A simulation model to predict seed dormancy loss in the field for *Bromus tectorum* L.

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Abstract

***Bromus tectorum* L. (cheatgrass) is an invasive winter annual whose seeds lose dormancy through dry after-ripening. In this paper a thermal after-ripening time model for simulating seed dormancy loss of *B. tectorum* in the field is presented. The model employs the hydrothermal time parameter mean base water potential ($\psi_b(50)$) as an index of dormancy status. Other parameters of the hydrothermal time equation (the hydrothermal time constant θ_{HT}, the standard deviation of base water potentials $\sigma_{\psi b}$, and the base temperature T_b) are held constant, while $\psi_b(50)$ is allowed to vary and accounts for changes in germination time-course curves due to stage of after-ripening or incubation temperature. To obtain hydrothemal time parameters for each of four collections, seeds were stored dry at 20 °C for different intervals, then incubated in water (0 MPa) or polyethylene glycol (PEG) solutions (−0.5, −1.0, −1.5 MPa) at 15 and 25 °C. Germination data for the thermal after-ripening time model were obtained from seeds stored dry in the laboratory at 10, 15, 20, 30, 40, and 50 °C for 0 to 42 weeks, then incubated at two alternating temperatures in water. Change in $\psi_b(50)$ was characterized for each collection and incubation temperature as a linear function of thermal time in storage. Measurements of seed zone temperature at a field site were combined with equations describing changes in $\psi_b(50)$ during after-ripening to make predictions of seed dormancy loss in the field. Model predictions were compared with values derived from incubation of seeds retrieved weekly from the field site. Predictions of changes in $\psi_b(50)$ were generally close to observed values, suggesting the model is useful for simulating seed dormancy loss during after-ripening in the field.**

Key words: After-ripening, cheatgrass, dormancy, hydrothermal time, thermal time.

Introduction

Many wild plants produce seed populations that exhibit dormancy. Models to predict field emergence of such species must generally address dormancy loss and induction as well as germination (Benech-Arnold and Sanchez, 1995). At present, few models exist to predict dormancy loss in the field (Baskin and Baskin, 1985; Benech-Arnold and Sanchez, 1995; Bouwmeester and Karssen, 1992; Karssen *et al*., 1988).

For the past several years, there have been attempts to understand and predict seed dormancy loss and germination timing for major wild species of the Intermountain Western United States (Allen and Meyer, 1990; Meyer, 1992; Meyer and Kitchen, 1992, 1994*a*, *b*; Meyer *et al*., 1989, 1990; Meyer and Monsen, 1992). More recently, attention has been focused on the weedy annual *Bromus tectorum* L. (Allen *et al*., 1995; Beckstead *et al*., 1996; Christensen *et al*., 1996; Meyer *et al*., 1997; Allen and Meyer, 1998). Commonly referred to as cheatgrass, Junegrass, or downy brome, *B. tectorum* is an introduced Eurasian grass which has invaded millions of hectares of wildland habitat and is considered by some to be the most significant plant invasion in North America (D'Antonio and Vitousek, 1992). The ability successfully to predict dormancy status and germination phenology of this species is fundamental to control and restoration efforts.

Seeds from different populations of *B. tectorum* exhibit different levels of dormancy at maturity, due to genetic variation among and within populations, as well as

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variation in environmental conditions during seed maturation (Milby and Johnson, 1987; Beckstead *et al.*, 1996; Meyer and Allen, 1995; Meyer *et al.*, 1997). Seeds lose dormancy through dry after-ripening during the summer and are then capable of germinating when sufficient moisture is present. A few published reports suggest that *B. tectorum* seeds are capable of persisting in the soil seed bank for more than a year (Wicks *et al.*, 1971; Young and Evans, 1975; Hull and Hansen, 1974). Preliminary field data from this laboratory indicate that the seeds are capable of entering secondary dormancy under certain conditions (Meyer and Carlson, unpublished data).

In this paper, a thermal after-ripening time model to simulate field dormancy loss in *B. tectorum* seeds is presented. The model uses the hydrothermal time parameter mean base water potential ($\psi_b(50)$) as an index of dormancy status.

Theory

The concept of hydrothermal time was proposed by Gummerson (1986) and further developed by Bradford (1990, 1995, 1996). Incubation time, temperature, and water potential conditions are used to determine progress toward germination, according to the equation

$$\theta_{HT} = (T_i - T_b)(\psi - \psi_b(g))t_g \quad (1)$$

where θ_{HT} is the hydrothermal time a seed requires for germination (e.g. MPa-degree-days), T_i and ψ are, respectively, temperature and water potential of the incubation medium, T_b is the theoretical base temperature at or below which germination will not occur, $\psi_b(g)$ is the theoretical base water potential at or below which germination of the g fraction will not occur, and t_g is the germination time of the g fraction. As the notation suggests, base temperature and hydrothermal time required for germination are considered constants for a seed population, while base water potential and germination time vary with germination fraction. The distribution of base water potentials within a population is assumed to be approximately normal, with mean $\psi_b(50)$ and standard deviation $\sigma_{\psi b}$. This assumption allows the germination time-course curve of a seed population to be characterized by the equation

$$\text{Probit}(g) = [\psi - \psi_b(50) - \theta_{HT}/((T_i - T_b)t_g)]/\sigma_{\psi b} \quad (2)$$

The probit value indicates the number of standard deviations away from the mean that any fraction of the population lies (e.g. in a normally distributed population 2.5% of the population is at least two standard deviations below the mean and 2.5% is at least two standard deviations above the mean). Furthermore, the probit transformation linearizes a cumulative normal distribution which facilitates modeling efforts (Bradford, 1990).

The model developed in this paper accounts for dormancy loss during after-ripening by changes in $\psi_b(50)$, which is allowed to vary with incubation temperature as well as after-ripening status. The other hydrothermal time parameters, θ_{HT}, $\sigma_{\psi b}$, and T_b, are held constant for a seed population during after-ripening. Changes in hydrothermal time parameters affect germination of a seed population upon hydration. A model with a single variable parameter was selected to simplify simulation of after-ripening in the field. Laboratory studies confirmed that $\psi_b(50)$ does indeed become more negative as seeds after-ripen (Christensen *et al.*, 1996), while other parameters apparently change very little during storage (Meyer and Allen, unpublished data).

In a previous article (Christensen *et al.*, 1996) dormancy loss (after-ripening) of two *B. tectorum* seed populations was modelled during laboratory storage at a single constant temperature (20 °C), as expressed at two incubation temperatures (15 and 25 °C) upon hydration. The parameter T_b was assumed to be 0 °C for each population. The parameters θ_{HT} and $\sigma_{\psi b}$ for each population were derived by a regression that combined germination time-courses obtained at different incubation temperatures, incubation water potentials, and stages of after-ripening. Values of $\psi_b(50)$ for each stage of after-ripening by incubation temperature combination were determined by adjustments to a single term in the regression model. A model of this type was developed for an additional seed collection (Potosi Pass) in conjunction with the present study (Fig. 1). As Fig. 1 illustrates, this approach is reasonably effective in describing dormancy loss during laboratory storage at a single constant temperature.

In order to develop a model that can account for the widely fluctuating temperatures that occur during after-ripening in the field, relationships between $\psi_b(50)$ and time in storage for each seed population were normalized on a common thermal time scale. Such a model assumes that the rate of change in $\psi_b(50)$ is a linear function of temperature above a base temperature according to the following equation:

$$\theta_{AT} = (T_s - T_l)t_{ar} \quad (3)$$

where θ_{AT} is the thermal time requirement for after-ripening, T_s is the temperature of storage, T_l is the lowest or base temperature (at or below which after-ripening does not occur), and t_{ar} is the time required for after-ripening, i.e. the time required for $\psi_b(50)$ to change from its initial value to its final value. As in any thermal time model, θ_{AT} is a constant, so that the time required for after-ripening decreases proportionately as the storage temperature increases above the base temperature.

Materials and methods

Seed harvest and dry storage

Mature florets (hereafter referred to as seeds) of *B. tectorum* were collected from four populations in the western USA

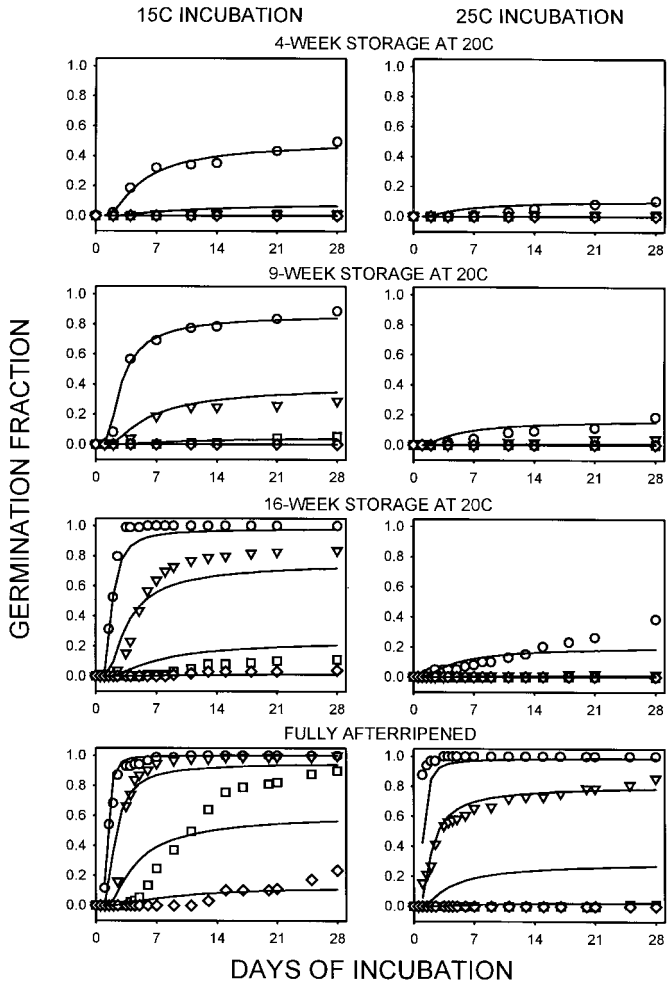

Fig. 1. Predicted and observed germination time-course curves for *Bromus tectorum* seeds of the Potosi Pass collection. Plotted curves were obtained by fitting a hydrothermal time model to observed laboratory data represented by symbols. The model was constrained to constant θ_{HT} and $\sigma_{\psi b}$, but $\psi_b(50)$ was allowed to vary as a function of after-ripening status and incubation temperature. Symbols and corresponding curves represent incubation at: 0 MPa (○); −0.5 MPa (▽); −1.0 MPa (□);and −1.5 MPa (◇). See Table 2 for parameter values.

during June and July of 1995 (Table 1). These populations were selected to represent a wide range of habitats and dormancy characteristics. In previous studies (Beckstead *et al.*, 1996; Meyer *et al.*, 1997), the warm desert Potosi Pass collection was highly dormant and slow to after-ripen, while the high montane Strawberry collection was largely non-dormant and fast to after-ripen. The Whiterocks and Hobblecreek collections, from cold desert and foothill habitats, respectively, were intermediate and variable in their dormancy characteristics. Within 2 weeks of harvest, following cleaning and drying, seeds at an initial water content of 8–10% (dry weight basis) were stored in sealed containers in dark constant temperature chambers.

Data for determination of hydrothermal time parameters

Incubation over a range of water potentials was carried out to provide data for determination of hydrothermal time parameters of each seed collection. Seeds for three of the collections (Whiterocks, Hobblecreek, and Potosi Pass) were incubated recently harvested (i.e. prior to dry storage) and following dry storage at 20 °C for multiple intervals. Seeds from each of these three collections, as well as seeds from the Strawberry collection, were also incubated following dry storage at 40 °C for 14 weeks, which was the treatment considered fully after-ripened (Christensen *et al.*, 1996). Seeds were incubated in 0, −0.5, −1.0, and −1.5 MPa polyethylene glycol (PEG) solutions at 15 and 25 °C. For additional details on this experiment refer to Christensen *et al.* (1996).

Data for determination of thermal after-ripening time parameters

Seeds for the thermal after-ripening time experiment were stored as described above at 10, 15, 20, 30, 40, and 50 °C. These temperatures represent the range of seed zone temperatures during summer at the field site (data not shown). Storage intervals at the different temperatures ranged from 1 to 42 weeks depending on expected after-ripening duration at a given temperature (Allen *et al.*, 1995; Meyer *et al.*, 1997). Subsamples of seeds were stored for up to 4 weeks at 50 °C, 6 weeks at 40 °C, 16 weeks at 30 °C, and 42 weeks at 20, 15 and 10 °C, with at least four storage intervals per temperature. Following storage, four replications of 25 seeds each were placed inside 10 cm diameter plastic Petri dishes on two paper germination blotters (Anchor Paper, St Paul, MN, USA) saturated with water. Stacks of Petri dishes were placed in plastic bags to reduce evaporative water loss, and water was added as necessary to maintain saturation of blotters during incubation. Seeds were incubated at 10/20 °C or 20/30 °C in chambers with 12 h alternating temperature and dark/fluorescent light regimes. Seeds were scored for germination (radicle emergence $\geq$1 mm) at days 1, 2, 4, 7, 11, 14, 21, and 28 of incubation. Following incubation, ungerminated seeds that were firm and turgid were scored as viable. Germination was calculated on the basis of percentage of viable seeds.

Field study

Field seed retrieval studies were carried out at Point of the Mountain, Utah, a sagebrush-grassland site with sandy loam soil (65.8% sand, 18.4% silt, 15.7% clay). Field and laboratory studies were started within a week of each other so that initial seed properties were approximately the same. Seeds harvested

Table 1. *Site information for collections of* Bromus tectorum *seeds used in experiments (adapted from Meyer* et al.*, 1997)*

Collection site (USA)	Ecological type	Elevation (m)	Plant community type	Mean annual precipitation (cm)	Mean temperature January (°C)	Mean temperature July (°C)
Whiterocks UT	Intermountain Desert	1450	Shadscale	17.7	−2.3	25.8
Hobblecreek UT	Intermountain Foothill	1800	Sagebrush-Gambel Oak	40.2	−2.1	24.8
Potosi Pass NV	Mojave Desert	1850	Blackbrush-Juniper	25.4	1.7	26.5
Strawberry UT	Intermountain Montane	2400	Subalpine Meadow	56.3	−7.8	16.1

as explained earlier from the each of the four study populations were air-dried, placed inside nylon mesh bags, and buried approximately 5 mm below the soil surface. Each bag contained approximately 200 seeds, as estimated by weighing. The bags were placed in four rows of 25 bags each, and four bags of each collection (one bag per row) were retrieved weekly from the site. Seeds were transported from the field to the laboratory (about 30 min transit time) in plastic bags to minimize changes in water content. Seeds were scored for field germination when necessary. The ungerminated seeds in each bag were divided into two approximately equal groups, one for each incubation temperature (10/20 °C and 20/30 °C), placed in dishes, incubated, and scored for laboratory germination and viability as described previously.

Temperature and water content of the seed zone (approximately the top 1 cm of soil) at the field site were measured using Thermistor (Omnidata, Logan, UT, USA) and Aquatel (Automata Inc., Grass Valley, CA, USA) sensors, respectively. Measurements were recorded hourly, as an average of six 10 min reads, using a data logger (Omnidata Easylogger 900, Logan, UT, USA). Aquatel sensors measure capacitance of the soil, which varies as a function of water content and soil characteristics. Laboratory calibrations were performed to determine water content values corresponding to Aquatel readings in Point of the Mountain soil. Corresponding water potential values were determined using a soil water release curve for this soil (Hanks, 1992).

Model development

Model development involved analysis of multiple data sets through a five-step process. The process is summarized here and developed in greater detail in the following paragraphs.

(1) Determine the hydrothermal time equations for each seed collection, using the germination time-course curves of seed sets incubated at different water potentials at two constant temperatures.

(2) Use hydrothermal time equations to calculate the $\psi_b(50)$ best characterizing each germination curve of seed sets stored dry at different temperatures or retrieved from the field, and incubated in water at two alternating temperature regimes.

(3) Characterize changes in the $\psi_b(50)$ value of a seed population over time as a function of dry storage temperature, and derive thermal time equations relating rate of change in $\psi_b(50)$ to storage temperature.

(4) Using the relationship derived between changes in $\psi_b(50)$ and storage temperature,predict changes in $\psi_b(50)$ of seeds after-ripening under measured temperature and water potential conditions in the field.

(5) To evaluate the success of the model, compare predictions of $\psi_b(50)$ under field after-ripening conditions to the $\psi_b(50)$ values obtained in step two for field retrieval seeds.

Hydrothermal time equation determination

The first step in model development was to determine the hydrothermal time parameters θ_{HT} and $\sigma_{\psi b}$, and the $\psi_b(50)$ values at two temperatures for fully after-ripened seeds of each seed collection. Parameter values for three of the populations (Whiterocks, Hobblecreek, and Potosi Pass) were obtained using data from multiple storage durations. This process is described in detail for the Whiterocks and Hobblecreek collections in Christensen *et al.* (1996). Values for the Strawberry seed collection were obtained using data from a single storage interval (fully after-ripened seeds), a technique suggested in our earlier paper (Christensen *et al.*, 1996). To determine hydrothermal time parameters, a probit regression model was created for each seed collection by collapsing germination curves obtained from incubation at two constant temperatures and a range of water potentials into a single analysis. The regression technique was based on Bradford (1990, 1995), with further refinements in Christensen *et al.* (1996). This results in an estimated $\psi_b(50)$ value for each incubation temperature by storage duration combination.

Calculation of $\psi_b(50)$ using hydrothermal time equations

The second step in model development involved calculating a $\psi_b(50)$ value for each germination time-course curve for seed sets stored dry in the laboratory or retrieved from the field, and then incubated in water. Once θ_{HT} and $\sigma_{\psi b}$ are determined for a seed population, the $\psi_b(50)$ best characterizing a single germination curve can be calculated from the relationship

$$\psi_b(g) = -\theta_{HT}/(T_i(t_g)) \quad (4)$$

This equation is derived from equation (1) where $T_b = 0$ and $\psi = 0$ (free water). Where seed germination of a specific treatment reached at least 50% of viable seeds, germination time of the 50% fraction, t_{50}, was used in equation (4) to obtain the $\psi_b(50)$ value. Values of t_{50} were obtained by linear interpolation between the two points surrounding the 50% fraction on each germination time course curve. Where cumulative germination did not reach 50% of viable seeds, alternative methods were required to estimate $\psi_b(50)$ of the seed set. When final germination was $>5\%$ and $<50\%$, the time to reach 75% of the final germination percentage (not total viable fraction) was linearly interpolated on the germination time course curve. This time value was then used in equation (4) to determine $\psi_b(g)$ of the relative 75% fraction. Next, a probit value for the relative 75% fraction was obtained from a probit table. For this application the probit value was always negative because all fractions were $<50\%$. The relationship between $\psi_b(g)$ and $\psi_b(50)$ is

$$\psi_b(g) = \psi_b(50) + (\text{probit}(g))(\sigma_{\psi b}) \quad (5)$$

By substituting the calculated value for $\psi_b(g)$, the known values for probit(g), and $\sigma_{\psi b}$ into equation (5), $\psi_b(50)$ was determined. Where final germination was 5%, $\psi_b(g)$

was assumed to be zero, and $\psi_b(50)$ was calculated from equation (5).

Development of a thermal after-ripening time model

The third step in model development was to characterize changes in $\psi_b(50)$ and therefore in dormancy status through time at the different storage temperatures, using a thermal after-ripening time model based on equation (3). A modification of the repeated regression procedure of Ellis *et al.* (1987) was used to estimate the values of thermal after-ripening time parameters. This involved plotting $\psi_b(50)$ values obtained at different storage temperatures and intervals for a given collection and incubation temperature against thermal time expressed as $(T_s - T_l)t$, varying the value of T_l until the best fit was obtained. $\psi_b(50)$ values obtained after dormancy loss was complete were eliminated from the analysis. The resulting linear equation took the form:

$$\psi_b(50) = m[(T_s - T_l)(t_{ar})] + b \quad (6)$$

The y-intercept (b) is the estimated initial value of $\psi_b(50)$, i.e. before any thermal time accumulation. The slope m is the decrement in $\psi_b(50)$ per unit of thermal time. The thermal time requirement for after-ripening (θ_{AT}) is obtained by rearranging equation (6) to determine the thermal time value, i.e. the value of $(T_s - T_l)t_{ar}$, when $\psi_b(50)$ reaches the value empirically determined to be the minimum or final value, i.e. the value for fully after-ripened seeds.

The thermal time requirement (θ_{AT}) is the thermal time required for $\psi_b(50)$ to change from its initial value (the value for recently harvested seeds) to its final value (the value for fully after-ripened seeds). The decrement in $\psi_b(50)$ per degree-hour can thus be expressed as:

$$\psi_b(50)_{decrement} = [(\psi_b(50)_{initial}) - (\psi_b(50)_{final})]/(\theta_{AT}) \quad (7)$$

This relationship can be used directly in the field simulation model of dormancy loss. The decrease in $\psi_b(50)$ in any interval of time is expressed as:

$$\psi_b(50)_{decrease} = [\psi_b(50)_{decrement}][(T_s - T_l)(t)] \quad (8)$$

The field seed zone temperature recorded for the 1 h time step is input for T_s, a value of 1 is input for time and constant values for $\psi_b(50)_{decrement}$ and T_l are input for a particular collection and incubation temperature.

Creation of simulation model to predict changes in $\psi_b(50)$ in the field

The fourth step in model development was to create a predictive model for the field using known seed zone temperature and water potential values, thermal after-ripening time parameters, and initial and final values for $\psi_b(50)$. The predictive model was created using Time-Zero software (Kirchner, 1990; Quaternary Software, Inc., Fort Collins, CO, USA), which writes a FORTRAN model built around predictive equations entered by the user. The model sequentially reads single lines of an input file containing hourly field seed zone temperatures and estimated seed zone water potentials. For each h increment (line of the data file), the model calculates the $\psi_b(50)$ decrease for a specific seed collection for each incubation temperature, using the corresponding thermal after-ripening time parameters. If estimated seed zone water potential during that h is considered low enough for after-ripening to proceed (below approximately -4 MPa), the $\psi_b(50)$ value of the population is decremented by the change in $\psi_b(50)$ due to after-ripening during that hour. The new $\psi_b(50)$ value is then saved as the $\psi_b(50)$ value of the population, and serves as the initial value for the next time step. The process continues until the $\psi_b(50)$ value of fully after-ripened seeds is reached. A -4 MPa cutoff value was used for after-ripening, because seeds may be able to accumulate progress toward germination above this water potential (Wilson, 1973). The exact value of the cutoff point is not critical to the after-ripening model, as seeds in the field spend relatively little time in this range of water potentials (Meyer and Allen, unpublished data).

Field validation of simulation model

The final step in modelling was to graphically compare predicted changes in $\psi_b(50)$ in the field for each seed collection at each incubation temperature with observed values obtained from weekly field retrievals.

Results

Overall, the four seed collections showed dormancy characteristics (as indicated by their hydrothermal time parameters) similar to the patterns observed for these populations in earlier studies (Table 2). Values of θ_{HT} varied by more than 2-fold among the collections. The value of $\sigma_{\psi b}$ was much larger for the Whiterocks collection than for the other three collections, which had similar $\sigma_{\psi b}$ values. A larger $\sigma_{\psi b}$ value indicates less uniform germination. The $\psi_b(50)$ values of recently harvested seeds showed large variation between incubation temperatures and among seed collections, while $\psi_b(50)$ values of fully after-ripened seeds were approximately constant across both incubation temperatures for all collections except Potosi Pass. The effect of constant versus alternating incubation temperatures on $\psi_b(50)$ was evident for recently harvested, but not for fully after-ripened seeds.

Changes in $\psi_b(50)$ through time for each collection as a function of storage and incubation temperature could be characterized quite well using a thermal after-ripening time model, with R^2 values from 0.75 to 0.92 (Fig. 2;

Table 2. *Hydrothermal time parameters for four* Bromus tectorum *seed collections*

Units of measurement are MPa-degree-days for θ_{HT}, and MPa for $\sigma_{\psi b}$ and $\psi_b(50)$ values.

	θ_{HT}	$\sigma_{\psi b}$	R^2	ψ_b (50) [recently harvested]				ψ_b(50) (fully after-ripened)	
				15 °C	25 °C	10/20 °C	20/30 °C	15 °C	25 °C
Whiterocks	43	0.60	0.90	−0.08	+0.77	−0.13	+0.50	−1.15	−1.15
Hobblecreek	35	0.33	0.83	−0.03	+0.17	−0.12	+0.14	−1.20	−1.20
Potosi Pass	22	0.36	0.82	+0.04	+0.86	+0.12	+0.84	−1.11	−0.81
Strawberry	52	0.31	0.79	–	–	−0.81	−0.16	−1.27	−1.27

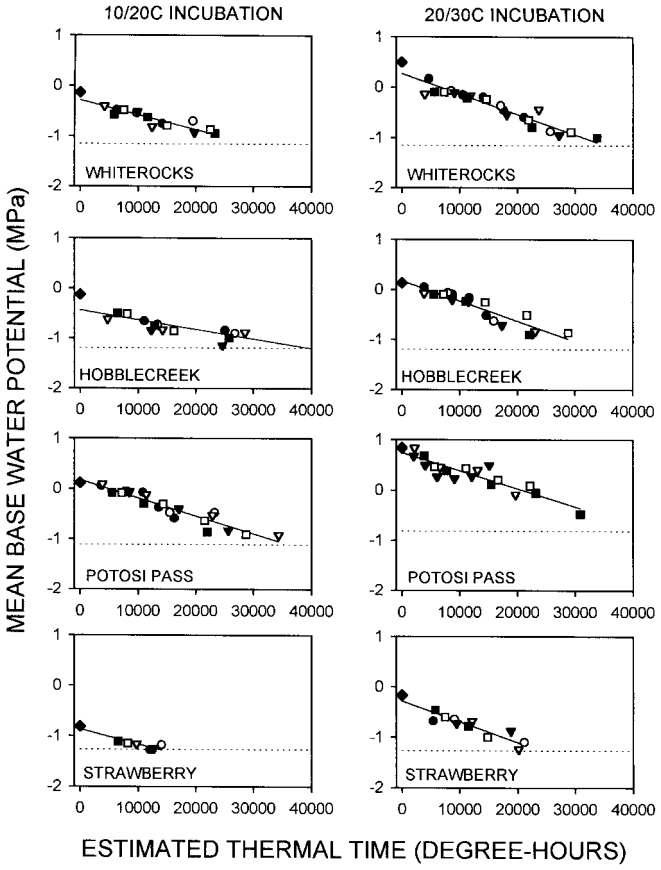

Fig. 2. Values of $\psi_b(50)$ plotted against thermal time elapsed in dry storage at a range of temperatures for four populations of *Bromus tectorum* as measured at two incubation temperatures. Storage regimes are: (◆) initial values, (●) 10 °C, (○) 15 °C, (▼) 20 °C, (▽) 30 °C, (■) 40 °C, and (□) 50 °C. The fitted line is the result of repeated regression analysis to obtain the base temperature with the best fit, the dotted horizontal line is the $\psi_b(50)$ value for fully after-ripened seeds, the slope of the regression line gives the decrement in $\psi_b(50)$ per unit of thermal time, and the intercept of the regression line with the dotted horizontal line gives θ_{AR}, the thermal time requirement for afterripening. See Table 3 for parameter values.

Table 3). Values for θ_{AT} were directly related to values of $[(\psi_b(50)_{initial})-(\psi_b(50)_{final})]$, resulting in $\psi_b(50)_{decrement}$ values that varied over less than a 2-fold range (Table 3). This means that collections that were more dormant initially had longer thermal time requirements for after-ripening, but that the rates of change during after-ripening were similar. More dormant collections generally had higher base temperatures for after-ripening as well as longer thermal after-ripening time requirements. This was especially evident in the Potosi Pass collection; its $\psi_b(50)$ at 20/30 °C remained essentially constant during 42 weeks of storage at temperatures at both 10 and 15 °C.

Predicted changes in $\psi_b(50)$ value due to after-ripening under field conditions were generally close to the values determined from germination time course curves of seeds from the field retrieval (Fig. 3). Values of $\psi_b(50)$ for seeds from recently harvested to 8 weeks in the field

Table 3. *Thermal after-ripening time parameters derived from repeated regression analysis using mean base water potential as the index of dormancy status, based on germination time-course data for four* Bromus tectorum *collections stored at six constant temperatures for periods of 0–42 weeks and incubated at two alternating tempteratures (see Fig. 2)*

Population	Incubation temperature	T_1 (base) temperature	θ_{AR} (degree-hours)	R^2	$P <$	Decrement (MPa-degree hour)	n
Whiterocks	10/20	6.7	27 552	0.76	0.001	−0.0000370	15
Whiterocks	20/30	6.5	33 518	0.92	0.001	−0.0000492	23
Hobblecreek	10/20	1.7	39 984	0.75	0.001	−0.0000270	17
Hobblecreek	20/30	7.1	32 960	0.88	0.001	−0.0000407	19
Potosi Pass	10/20	7.3	35 403	0.90	0.001	−0.0000380	23
Potosi Pass	20/30	17.0	42 098	0.85	0.001	−0.0000392	20
Strawberry	10/20	1.5	13 670	0.85	0.02	−0.0000337	7
Strawberry	20/30	6.0	23 995	0.86	0.001	−0.0000463	12

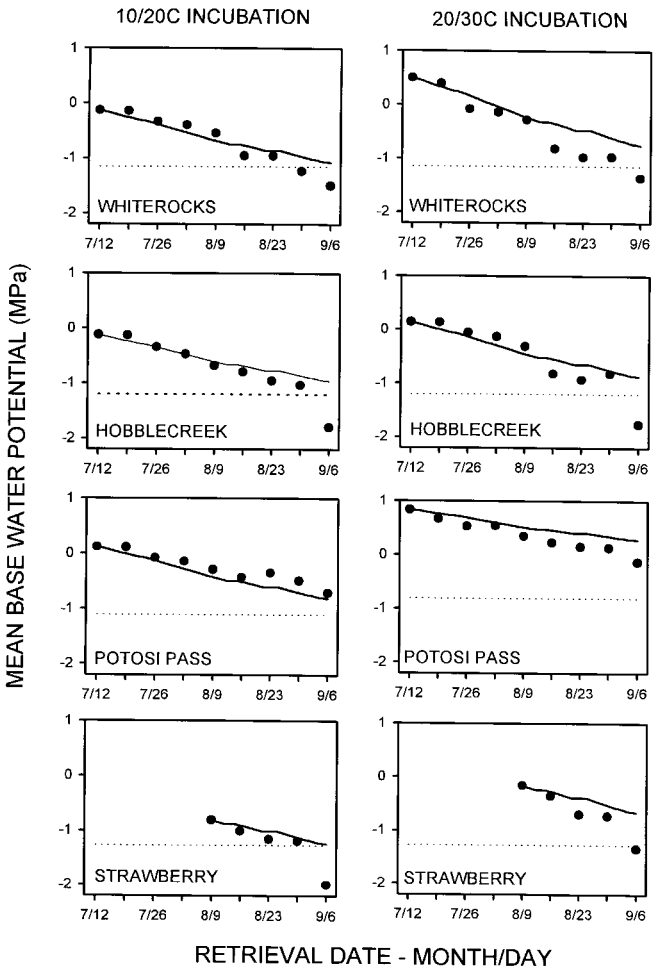

Fig. 3. Predicted and observed changes in $\psi_b(50)$ during field after-ripening for seeds from four populations of *Bromus tectorum* as measured at two incubation temperatures. Symbols represent measured laboratory values for seeds retrieved from the field, solid lines represent values predicted from simulation modelling, and dotted horizontal lines represent $\psi_b(50)$ values of fully after-ripened seeds for each seed collection and incubation temperature.

are included in the retrieval plots for Whiterocks, Hobblecreek, and Potosi Pass. The Strawberry seed collection ripened later than the other collections because of the subalpine habitat (Table 1). For this reason, only 4 weeks of after-ripening in the field could be included before the seeds began to progress toward germination following rainfall events.

The last recorded observed values of $\psi_b(50)$ fall below the predicted values of fully after-ripened seeds in all collections except Potosi Pass (Fig. 3). These observed values are spurious, because seeds approaching fully after-ripened status in the field had progressed significantly toward germination due to precipitation, thus reducing their remaining hydrothermal time requirement. Consequently, predicted and observed $\psi_b(50)$ values were not compared beyond this point. The spurious values are included here to indicate the effect of progress toward germination on calculating $\psi_b(50)$ values. Calculation of $\psi_b(50)$ from equation (4) is not valid once seeds have accumulated significant hydrothermal time. In a complete simulation model for predicting germination phenology in the field, this is the point at which the field dormancy loss model would be linked to a hydrothermal time model for predicting germination phenology.

Discussion

Several decisions were made during the course of model building to meet the challenges that were encountered. Many of these decisions required assumptions, whether theoretical or necessary from a practical standpoint. The ability of the model successfully to predict rates of dormancy loss in the field suggests that the use of these assumptions was appropriate.

This model is based on the previously-verified assumption (Christensen *et al.*, 1996) that differences in germination time-course curves of a seed population due to after-ripening and incubation temperature can be described by the single variable $\psi_b(50)$, holding θ_{HT}, $\sigma_{\psi b}$, and T_b constant for the population. This approach does not give the best fit for each individual curve, but creates a useful general model (Table 2; Fig. 1).

The modelling process is based on the decision that changes in $\psi_b(50)$ through time at different storage temperatures can be represented using thermal after-ripening

time. This requires the assumption that changes in $\psi_b(50)$ through time at any storage temperature are approximately linear. This assumption contradicts the observation in Christensen *et al.* (1996) that changes in $\psi_b(50)$ during after-ripening at 20 °C were not linear, but were more rapid early during after-ripening. However, with the considerably greater data set available for the present study (133 data points versus eight in Christensen *et al.*, 1996), it was concluded that there is no basis for considering this relationship to be non-linear.

Using a repeated regression analysis that incorporated data points from later in the after-ripening process gave a better fit to the field observations than a thermal time model based on interpolation of halfway times (data not shown). In a previous paper interpolated mean time indices were used to characterize changes in three other indicators of dormancy loss in *B. tectorum* (dormant seed percentage, mean germination time of the germinable fraction, and synchrony index; Allen *et al.*, 1995). Mean or halfway times were then plotted for these three indices against temperature and fitted the relationships with negative exponential equations. Inverse functions and negative exponential functions generate very similar curves. It is therefore likely that the relationships between rate of change during storage in those dormancy indices could also have been fit successfully with a thermal after-ripening time model. Similarly, the mean dormancy period in six cultivars of rice was shown to be a negative log-linear function of storage temperature (see Roberts, 1965; and Fig. 7 in Roberts, 1988), suggesting that a thermal after-ripening time model could be applied to those data as well. The dormancy loss model presented in Christensen *et al.* (1996) and extended here incorporates the effects observed in earlier work (Allen *et al.*, 1995), as the three dormancy indices used in that work change simultaneously in concert with underlying changes in $\psi_b(50)$.

Model development also required decisions on how seed zone temperature and water potential could best be used to predict field after-ripening. The model contains the assumption that the effect of fluctuating seed zone temperatures is equivalent to a summation of the effects of short constant temperature intervals. Another decision was to ignore the effect of water potential over the dry after-ripening range. Previous studies have shown that seed water potential can affect after-ripening rates (Leopold *et al.*, 1988; Foley, 1994). The laboratory data, based on storage over a range of saturated salt solutions, show that *B. tectorum* seeds after-ripen at a uniform rate over a wide range of water potentials above −150 MPa, and only exhibit delayed after-ripening at water potentials below this threshold (unpublished data). The success of this temperature-only model indicates that seed water potentials were generally above −150 MPa during dry after-ripening in the field.

To incorporate effects of higher soil water potentials, an upper threshold value for after-ripening was chosen. No changes in hydrothermal time parameters due to water potentials above the threshold (i.e. from rainfall) are included in the model. During early stages of after-ripening, seeds progress relatively little toward germination during periods of high soil water potential, because of their high $\psi_b(50)$ values. During later stages of after-ripening, seeds accumulate greater progress toward germination during periods of high soil water potential, confounding the after-ripening effect (Fig. 3). Once obvious progress toward germination has occurred (e.g. spurious values of $\psi_b(50)$ for field retrievals, observed germination in the field), the after-ripening model can no longer be applied. Extension of this model to predict field germination would require application of a method to account for accumulation of hydrothermal time by partially after-ripened as well as fully after-ripened seeds.

Model building resulted in several insights into characteristics of *B. tectorum* seed populations. The $\psi_b(50)$ values for recently harvested seeds generally varied among populations at each incubation temperature (Table 2). The initial $\psi_b(50)$ value largely determined how quickly seeds reached fully after-ripened status in the field. Comparison of the field after-ripening plots (Fig. 3) shows that after-ripening of seeds in the field occurred at a relatively constant rate across seed collections and incubation temperatures. This uniformity in slopes is largely due to the fact that seed collections after-ripened at similar rates at the high temperatures prevailing during the summer of 1995. Lower field seed zone temperatures would have resulted in more divergent slopes due to an accentuation of the effect of differences in base after-ripening temperatures.

Constancy or variation of $\psi_b(50)$ values across incubation temperatures gives an indication of the optimum germination temperature. When two incubation temperatures are both below optimum, differences in germination can be accounted for by thermal time only, and $\psi_b(50)$ values are approximately the same for both incubation temperatures. When at least one incubation temperature is above optimum, differences in germination between incubation temperatures cannot be explained by thermal time only, and require variation in $\psi_b(50)$ values for explanation. The constancy of $\psi_b(50)$ values across the incubation temperatures 15 °C and 25 °C (Table 2), suggests that fully after-ripened seeds of the Whiterocks, Hobblecreek and Strawberry collections have an optimum temperature above 25 °C. Variation in $\psi_b(50)$ values between incubation temperatures shows that recently harvested seeds of all collections, and fully after-ripened seeds of the Potosi Pass collection, have an optimum temperature below 25 °C.

The $\psi_b(50)$ values of fully after-ripened seeds were apparently not affected by whether incubation temper-

atures with the same mean were constant or alternating, but this was not true for recently harvested seeds (Table 2). The difference in effect between recently harvested and fully after-ripened seeds may have resulted from decreased requirements for specific incubation conditions (e.g. alternating temperatures) in after-ripened seeds.

A major limitation of this thermal after-ripening time model in its present form is the fact that each incubation temperature requires a unique set of parameters. It is tempting to speculate that a more general thermal after-ripening time model could be built by assuming that the base temperature for after-ripening and the slope of the change in $\psi_b(50)$ are constant across incubation temperatures. This would mean that the difference between the initial and final $\psi_b(50)$ values would be the only variable affecting the value of θ_{AT} at each incubation temperature. It has been demonstrated that this more general model applies to the after-ripening process in another grass species of the sagebrush steppe (*Elymus elymoides*, bottlebrush squirreltail; Debaene *et al*., unpublished results). Unfortunately, analysis of covariance for *B. tectorum* collections in the present study, with incubation temperature as the class variable and thermal time in storage as the continuous variable, indicates that the slopes of change in $\psi_b(50)$ at different incubation temperatures are not identical, whether or not the model is constrained to a common base temperature for after-ripening (data not shown). The apparently complex relationship between incubation temperature and after-ripening rate in this species will require clarification with data from a more comprehensive set of incubation temperatures.

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