Weed Science, 52:518–524. 2004

Predicting timing of downy brome (*Bromus tectorum*) seed production using growing degree days

Daniel A. Ball
Corresponding author. Columbia Basin Agricultural Research Center, Oregon State University, P.O. Box 370, Pendleton, OR 97801;
daniel.ball@oregonstate.edu

Sandra M. Frost
Columbia Basin Agriculture Research Center, Oregon State University, Pendleton, OR 97801

Alix I. Gitelman
Statistics Department, Oregon State University, Corvallis, OR 97331

Downy brome in dryland winter wheat presents a major constraint to the adoption of reduced tillage cropping systems in the Pacific Northwest of the United States. Effective suppression of downy brome during fallow periods depletes seed in the soil and reduces infestations in subsequent winter wheat crops. Delayed tillage operations or delayed herbicide applications in the spring increase the risk for production of viable downy brome seed during fallow periods. In a series of studies, downy brome panicles were sequentially sampled at Pendleton, OR, and Pullman, WA, in 1996 and 1997, and at nine locations around the winter wheat growing region of the western United States in 1999 and 2001. Cumulative growing degree days (GDD) were calculated using local, daily maximum, and minimum air temperature data. A simple GDD model based on the formula GDD = (daily maximum temperature [C] + daily minimum temperature [C])/2, with a base temperature of 0 C and a starting point of January 1, was used to calculate cumulative GDD values for panicle sampling dates. Number of seed germinating per collected panicle was recorded in greenhouse germination tests. Estimations of degree days required for production of viable downy brome seed were made using nonlinear regression of germination on GDD. The GDD value at which viable seed can be found on plants (i.e., when seed germination > 0) was of interest. Estimates of the GDD values at which viable seed could be found in the three studies ranged from 582 GDD at Bozeman, MT, to 1,287 GDD at Stillwater, OK, with a group of GDD values for Pendleton and Pullman around 1,000. Variation in seed-set GDD among locations may be attributed to differing climatic conditions that control vernalization at the various locations or to differences in vernalization requirements among downy brome biotypes (or both).

Nomenclature: Downy brome, *Bromus tectorum* L. BROTE; winter wheat, *Triticum aestivum* L. TRZAW.

Key words: Seed development, growing degree days, modeling, cheatgrass.

Infestations of downy brome present a major constraint to the adoption of conservation tillage systems in dryland winter wheat–fallow cropping regions of the Pacific Northwest of the United States. Moldboard plowing, which buries weed seed (Ball 1992; Yenish et al. 1992), has long been the conventional practice for managing downy brome in this region. However, moldboard plowing reduces plant residues on the soil surface. Conservation tillage increases surface crop residues, thus reducing soil erosion, but leaves weed seed on the soil surface. Selective herbicides for downy brome control in winter wheat have potential to cause development of herbicide-resistant downy brome populations (Ball and Mallory-Smith 2000; Mallory-Smith et al. 1999) or to provide only partial suppression (Pacific Northwest Weed Management Handbook 2002). For these reasons, multiple year crop rotations, including spring-seeded crops and fallowing, are necessary for the integrated management of downy brome (Blackshaw 1994; Daugovish et al. 1999). Precipitation patterns vary greatly throughout the inland Pacific Northwest and can make spring-seeded crops an economically risky option for some growers using currently available farming practices. Economics, conservation efforts, climate, and herbicide resistance concerns, all complicate efforts to manage downy brome in the winter wheat–fallow crop production areas of the Pacific Northwest.

Integrated management of downy brome in wheat cropping systems includes prevention of downy brome seed production both in years when spring crops are grown and during fallow periods to reduce downy brome population density in subsequent winter wheat crops. Delaying fallow tillage operations or herbicide applications in spring increases the risk for production of viable downy brome seed during the fallow period.

A more precise understanding of reproductive development of downy brome, particularly with regard to when viable seed production occurs (seed set), could enhance downy brome management through improved timeliness of control operations in fallow. Specifically, if the "cutoff" date for prevention of downy brome seed production was known, managers could more effectively schedule field operations to prevent downy brome seed production. The understanding of seed-set time in downy brome also would be helpful for timing downy brome control in rangeland environments.

Vegetative and reproductive developmental stages of winter wheat and other grasses, including downy brome, have been related to growing degree days (GDD) on the basis of air temperature (Ball et al. 1995; Dotray and Young 1993; Klepper et al. 1982, 1984). Vegetative development of other weeds also has been related to GDD (Deen et al. 1998; Wilen et al. 1996). The development rate for downy brome is more rapid than wheat but overall developmental relationships to GDD are very similar to wheat (Ball et al.

Table 1. Panicle sampling dates and mean downy brome seed germination per panicle in 1996 at Pendleton, OR, and Pullman, WA.

Pendleton, OR			Pullman, WA		
Date	Cumulative GDD[a]	Germinated seeds per panicle	Date	Cumulative GDD	Germinated seeds per panicle
May 28	1,061	3	May 28	785	0
May 31	1,096	8	May 31	811	0
June 3	1,150	20	June 3	861	0
June 10	1,270	48	June 6	910	0
June 17	1,386	69	June 10	982	1
			June 13	1,024	0
			June 27	1,223	69

[a] Abbreviation: GDD, growing degree days.

1993). Therefore, models for winter wheat growth could likely be modified to estimate dates of downy brome seed production.

The role of photoperiod in controlling floral development in downy brome has not been defined. However, the time of reproductive development for downy brome under natural conditions is during increasing day length regardless of the range of latitude, which should minimize the probability that day length is a factor controlling floral development.

There is uncertainty about when to begin the calculation of cumulative GDD. Because downy brome seedling emergence cannot be known precisely under field conditions, cumulative GDD calculation beginning at emergence is not practical. Crops of winter wheat sown at widely different dates tend to ripen at the same time the following summer (Hay and Kirby 1991). For this study, it was assumed that downy brome follows this same convergence of plant development and has vernalized by January 1. We used cumulative GDD beginning January 1 to predict time of downy brome seed set.

Multiple studies were conducted to establish the relationship between time of downy brome seed production and cumulative GDD and to determine the applicability of this relationship over a broad geographic range. A 1996 study investigated the effect of location on time of downy brome seed set within the Pacific Northwest. A 1997 study investigated the effects of planting date and biotype on time of downy brome seed set. A study conducted in 1999 and repeated in 2001 investigated seed-set timing over a broad geographic distribution around the wheat-producing region of the western United States. The objective of this study is to report and interpret the GDD results from these three studies and to develop a model to predict seed set in downy brome.

Materials and Methods

Pendleton–Pullman, 1996

In an initial study, downy brome panicles were randomly sampled at intervals from naturally occurring stands of downy brome growing in summer fallow fields at the Columbia Basin Agricultural Research Center near Pendleton, OR (N45°43.2′ W118°37.6′) and from a downy brome seed nursery at the Spillman Conservation Field Station near Pullman, WA (N46°41.713′ W117°8.60′). Downy brome panicles were sequentially collected during the spring and early summer of 1996 to determine the cumulative GDD required to obtain viable downy brome seed production. At each sampling date at both locations (Table 1), three randomly selected, replicate samples of 30 downy brome panicles were clipped just below the point of rachis attachment and placed in paper bags. Daily maximum and minimum temperatures for the year were recorded at both locations.

Collected panicles were dry-stored in the laboratory for approximately 6 mo to improve germination of harvested downy brome seed (Thill et al. 1980). After the 6-mo afterripening period, seed was cleaned by gently rubbing intact panicles on a textured rubber mat. Collected seed was sown in 5-cm-deep flats containing a standard greenhouse soil mix, placed in a greenhouse maintained at 21/18 C day/night temperatures, with 16 h of daylight, and watered daily. Germination data were recorded as seed germinated per panicle 14 d after planting (Table 1) because the objective was to find the point in time when viable seed could be found in the sampled population rather than to describe seed germination per se.

Cumulative GDD were calculated using local, daily maximum, and minimum air temperature data. A simple model was used to calculate cumulative GDD values for each sampling date (following Klepper et al. 1988):

Table 2. Sampling dates and mean downy brome germination per panicle of four downy brome biotypes for each date in 1997 for Pendleton, OR, and Pullman, WA, averaged across planting dates.

Pendleton, OR						Pullman, WA					
Date	GDD[a]	Imbler	LaCrosse	Pendleton	Pullman	Date	GDD	Imbler	LaCrosse	Pendleton	Pullman
		Seeds/panicle						Seeds/panicle			
May 14	854	0	0	0	0	May 30	829	0	0	0	0
May 16	893	0	0	0	0	June 2	874	0	0	0	0
May 19	934	0	0	0	0	June 6	927	0	0	0	0
May 23	983	0	0	0	0	June 9	971	0	0	0	0
May 27	1,040	5	5	3	1	June 13	1,034	2	1	1	1
May 31	1,110	8	16	10	4	June 16	1,093	5	4	4	5
June 3	1,154	21	24	26	14	June 19	1,140	13	10	8	8
June 5	1,181	29	34	41	17	June 24	1,206	16	18	28	10
June 9	1,239	24	30	40	16	June 27	1,253	26	29	30	26
June 11	1,274	40	31	56	39	July 2	1,327	39	44	35	32

[a] Abbreviation: GDD, growing degree days.

Table 3. Sampling dates and mean downy brome germination per panicle for each date for western U.S. sites in 1999 and 2001.

1999														
Pendleton, OR			Hays, KS			Sidney, NE			Stillwater, OK			Moccasin, MT		
Date	GDD[a]	S/p	Date	GDD	S/p	Date	GDD	S/p	Date	GDD	S/p	Date	GDD	S/p
May 10	839	0	May 7	831	0	May 18	550	0	April 15	947	0	May 21	530	0
May 14	880	0	May 11	903	1	May 21	593	0	April 19	995	0	May 28	637	0
May 19	942	0	May 14	947	14	May 24	635	0	April 23	1,067	0	June 3	712	0
May 24	1,009	1	May 18	1,020	39	May 27	679	0	April 27	1,129	0	June 10	789	1
May 27	1,056	21	May 21	1,079	101	June 3	787	11	April 30	1,177	4	June 19	923	91
June 1	1,136	48	May 25	1,156	158	June 7	855	56	May 4	1,254	6	June 24	1,010	142
June 4	1,176	34	May 28	1,204	171	June 9	898	61	May 7	1,299	16	June 29	1,081	155
June 7	1,224	49	June 1	1,289	168	June 14	973	138	May 11	1,378	117			

[a] Abbreviations: GDD, growing degree days; S/p, seeds germinated per panicle.

$$\text{GDD} = (\text{daily maximum temperature} + \text{daily minimum temperature})/2$$

where temperatures were recorded (in C). If the resulting daily GDD value was negative, it was reset to zero (base temperature). Cumulative GDD was calculated from January 1 by totaling daily GDD values. For each site j, cumulative GDD is denoted X_{ij}, where i indexes the samples within site j. The response variable for each sample on each sampling date for site j, denoted Y_{ij}, was taken to be number of seed germinated per panicles collected. A nonlinear regression model (using PROC NLIN; SAS Institute Inc. 1989) was fit to the data at each site to determine the cumulative GDD value at which seed germination occurred (i.e., the GDD seed set). For each site, this model takes the form:

$$Y_{ij} = \hat{a}_j[\max\{(X_{ij} - \grave{e}_j),0\}] + \mathring{a}_{ij} \quad [1]$$

where $\grave{e}_j$ denotes the cumulative GDD value at which seed set occurs for site j; $\hat{a}_j$, the slope of the relationship between cumulative GDD and seed germination after seed set for site j; and $\mathring{a}_{ij}$, the independent normal error terms with mean zero and variance $\acute{o}^2{}_j$. This model is nonlinear because Y_{ij} is a nonlinear function of the parameters $\grave{e}_j$ and $\hat{a}_j$.

Biotypes at Pendleton–Pullman, 1997

A second study was conducted during 1997 to investigate the effects of planting date and biotype on downy brome seed set. The study had a two-factor factorial treatment arrangement, set in a randomized complete block experimental design, at two locations and was analyzed as a series of studies. Planting time (October, December) and downy brome biotype (4) were the two factors. Dry-stored seed from four downy brome biotypes collected near Imbler, OR, Pendleton, OR, LaCrosse, WA, and Pullman, WA, were planted at the Pendleton and Pullman locations, the same two sites described for the previous study. Planting dates were October 25 and December 2, 1996 at Pendleton and October 30 and December 12, 1996 at Pullman.

Field sites were cultivated before sowing to prepare a fine seedbed. Seed was sown in rows, 1 cm deep and 150 cm apart. Individual plots consisted of a single 6-m-long section of row in a randomized complete block arrangement with four replications. Daily maximum and minimum air temperatures were recorded from planting at both the locations with an Optic StowAway® Temperature logger.[1] At each sampling time (Table 2), beginning at approximately 50% panicle emergence and continuing at approximately 50 GDD intervals, all panicles in a randomly selected 0.6-m row were harvested by hand-clipping panicles at the point of rachis attachment. Panicles were counted and dry-stored in brown paper bags for approximately 6 mo to allow afterripening and reduce dormancy.

After completion of the afterripening period, seed samples were cleaned to remove chaff, sown in flats filled with a standard greenhouse potting mix, and grown in the greenhouse as described for the first study. Downy brome seedlings in each flat were counted 14 d after planting. Seed germination per panicle and cumulative GDD (Table 2) were calculated as in the first study. Seed-set GDD were estimated for each replicate at each location with the PROC NLIN procedure. Estimated seed-set GDD values were weighted because of heterogeneity of variance among seed-set estimates. Differences in estimated seed-set GDD values among biotypes were evaluated with analysis of variance (ANOVA) procedures ($\alpha = 0.05$).

Western Region, 1999 and 2001

In a third study conducted in 1999 and 2001, developing downy brome panicles were randomly sampled at intervals at nine locations around the winter wheat growing region of the western United States (Table 3). Locations included Pendleton, OR; Hays, KS; Sidney, NE; Stillwater, OK; Moccasin, Havre, and Bozeman, MT; Ft. Collins, CO; and Moscow, ID. Data from the nearest weather recording stations were used to determine cumulative GDD required for downy brome seed set. Two years of data were collected at four sites: Pendleton, OR; Hays, KS; Sidney, NE; and Stillwater, OK; whereas data for 1999 only were collected at five sites: Moccasin, Havre, and Bozeman, MT; Moscow, ID; and Ft. Collins, CO (Table 3). Data collected in 2001 for Bozeman and Moccasin, MT, were not used because seed set had occurred before the first collection date. Downy brome panicles were clipped below the point of rachis attachment from naturally occurring populations growing in winter wheat, fallow, or along field margins. Collected seed were dry-stored for 6 mo and germinated in the greenhouse as described previously. Seed germination per panicle and cumulative GDD from January 1 were calculated as in the previous studies (Table 3). As in the earlier studies, seed-set GDD values were estimated using the PROC NLIN procedure.

TABLE 3. Extended.

1999											
Havre, MT			Bozeman, MT			Ft. Collins, CO			Moscow, ID		
Date	GDD	S/p	Date	GDD	S/p	Date	GDD	S/p	Date	GDD	S/p
May 21	579	0	May 27	583	0	May 26	806	0	May 27	730	0
May 28	713	0	June 7	710	3	May 28	836	2	May 31	783	1
June 9	890	0	June 14	791	30	June 1	902	13	June 5	841	14
July 13	1,462	48	June 18	860	12	June 4	958	44	June 10	887	11
			June 24	963	13	June 14	1,121	145	June 14	955	73
			July 9	1,188	48	June 20	1,228	134	June 17	1,018	111
			July 16	1,321	85				June 21	1,080	128
			July 30	1,612	58				June 25	1,139	112

Results

A nonlinear regression model was effective for the objectives of these three studies because it allowed for estimation of a "change-point" value ($\grave{e}_j$)—the cumulative GDD value at which seed germination becomes nonzero. The PROC NLIN procedure uses an iterative algorithm to estimate both this change-point value ($\grave{e}_j$) and the slope term ($\hat{a}_j$) that describes the relationship between cumulative GDD and seed germination after the change point. As with any iterative algorithm, starting values for the NLIN procedure are required. These starting values can be thought of as crude estimates for the parameters of interest—the change point ($\grave{e}_j$) and the postchange-point slope ($\hat{a}_j$). Depending on the sample size within locations and the variability of the cumulative GDD within locations, the NLIN procedure can be sensitive to these starting values. For that reason, in the results reported below, starting values for the NLIN procedure also are provided. Furthermore, all regressions were significant at levels greater than 0.01 and had r^2 values ranging from 1.0 (Pullman 1996) to 0.54 (Stillwater 2001).

Pendleton–Pullman, 1996

Panicle collection at Pullman began on May 28, 1996 (785 GDD), before downy brome seed set. The change point was not calculated from the 1996 Pendleton data because downy brome seed had already set at Pendleton before the first sample date on May 28, 1996 (Table 1). Regression of seed germination per panicle data over GDD using the PROC NLIN procedure for 1996 Pullman produced a seed-set estimate of 1,023 GDD (SE = 2.24 GDD, $\hat{a}_j = 0.5$, $\grave{e}_j = 1{,}000$) (Table 4).

Biotypes at Pendleton–Pullman, 1997

An initial collection of downy brome panicles at the Pendleton site was made on May 14 after accumulation of 854 GDD. At this sampling time, no viable downy brome seed were found. Germinable seed of all four biotypes were first found at Pendleton in a May 27 sampling after accumulation of 1,040 GDD and at all subsequent sampling dates (Table 2). At the Pullman site, the first germinable downy brome seed were found after accumulation of 1,034 GDD from panicle samples taken on June 13, 1997. Seed-set GDD estimates were calculated for all combinations of locations, biotypes, and planting dates using PROC NLIN procedures.

The results of ANOVA on the weighted seed-set GDD estimates suggested a minor biotype by location interaction. Interaction means were separated using least square means (LSMeans) procedures in SAS. Specifically, the GDD seed-set estimate for the LaCrosse biotype grown at Pendleton was significantly different from the GDD seed-set estimate for LaCrosse grown at Pullman (Table 4). In addition, GDD seed set for the LaCrosse seed grown at Pendleton differed from Pullman seed grown at either location. However, estimates of seed set for the LaCrosse biotype are around 1,000 GDD (Figure 1). It would be interesting to have a GDD seed-set estimate for the LaCrosse biotype in its own niche. Time of downy brome seed set was not influenced by planting date, so seed-set GDD estimates were averaged across planting time (Table 2). The GDD seed-set estimates were similar for Pendleton and Pullman seed at both locations. Seed-set GDD estimated values for all biotypes at both locations, with the exception of LaCrosse biotype at Pendleton, were above 1,000 GDD ($\hat{a}_j = 0.5$, $\grave{e}_j = 900$) (Table 4). Furthermore, absence of an effect for planting date suggests that using January 1 for beginning the accumulation of GDD is appropriate, at least for these two locations.

Western Region 1999 and 2001

Estimates of GDD seed set at these nine sites (starting values of $\hat{a}_j = 0.5$, $\grave{e}_j = 850$ for all sites except Stillwater. Stillwater starting values ($\hat{a}_j = 0.5$, $\grave{e}_j = 1{,}200$) encompass a wider range of values than that of the Pendleton–Pullman sites (Figure 1; Table 4). Downy brome at most of the sites set seed at lower cumulative GDD than did downy brome at Pendleton or Pullman. However, downy brome at Stillwater, OK, set seed at higher cumulative GDD than at any other location.

A figure of the GDD seed-set estimates obtained from all three studies illustrates the relationship of these estimates across locations (Figure 1). Each horizontal line in this figure depicts a GDD seed-set estimate ± 2 SE for that estimate. The multiplier two was chosen to control for the pairwise comparison error rate, under an assumption that the GDD seed-set estimates approximate, roughly, normal distributions. In this figure, locations for which error bars substantially overlap, such as Havre and Ft. Collins, are not suggestive of a difference in GDD seed set. In contrast, locations for which error bars do not overlap suggest a difference in GDD seed set for those locations. In particular, the Boze-

Table 3. Extended.

2001											
Pendleton, OR			Hays, KS			Sidney, NB			Stillwater, OK		
Date	GDD	S/p	Date	GDD	S/p	Date	GDD	S/p	Date	GDD	S/p
May 16	805	0	May 1	668	0	June 3	864	0	April 19	804	0
May 21	866	0	May 6	741	1	June 7	920	3	April 24	896	0
May 25	949	0	May 11	834	3	June 10	984	12	April 26	931	0
May 29	1,023	6	May 14	900	39	June 12	1,026	61	May 1	1,032	1.6
June 1	1,071	8	May 18	988	67	June 15	1,066	72	May 2	1,056	1.8
June 4	1,115	4	May 22	1,054	81	June 18	1,127	134	May 7	1,159	0.5
June 8	1,179	—	May 25	1,092	98	June 20	1,154	139	May 11	1,241	0.1
June 11	1,228	—	May 30	1,180	92	June 23	1,217	78	May 14	1,309	5.0

man estimate and both Stillwater estimates appear to stand out as different from those at other locations.

The average of the six GDD seed-set estimates from Pendleton (four biotypes from 1997, one from 1999, and one from 2001) is 999 GDD. The average of the five estimates from Pullman (one in 1996, four biotypes in 1997) is 1,077 GDD. Combining Pendleton and Pullman yields an average of 1,034 GDD for seed set. These averages, combined with the finding of no difference between Pendleton and Pullman in the second study, suggest that a 1,000 GDD seed-set value could be adopted for a Pacific Northwest downy brome management model. Using official National Oceanographic and Atmospheric Administration data, a 20-yr average date for a heat accumulation to 1,000 GDD was calculated for both Pendleton (May 23) and Pullman (June 11). Together, these calculations suggest that managers in the Pendleton area use a mid-May cutoff date for implementing downy brome management plans, whereas those in the Pullman area use an early June cutoff date. An interactive Web site has been developed to calculate real-time, cumulative GDD for the inland Pacific Northwest. This site is accessed at http://pnwpest.org/cgi-bin/nwmapmaker.pl and is useful for visualizing cumulative GDD for a given Pacific Northwest location.

Discussion

These data support the hypothesis that seed development can be related to cumulative GDD at a given geographic location. However, when observed over a broader geographic range (i.e., Bozeman to Stillwater), the simple model developed for one location will require adjustment for use in another location. Data will need to be transformed to model timing of seed development over wide geographic ranges. Differences in downy brome GDD seed set among locations may be attributed to climatic differences affecting the rate

Table 4. Estimated downy brome seed set at 10 western U.S. sites.

Location	Year	Seed set	Standard error	Estimated date of seed set	20-year average date to reach 1,000 GDD[a]
		GDD			
Pullman, WA	1996	1,023	2	June 15	June 11
Imbler	1997	1,027	44	June 12	June 11
LaCrosse	1997	1,151	30	June 20	June 11
Pendleton	1997	1,105	22	June 17	June 11
Pullman	1997	1,077	22	June 16	June 11
Pendleton, OR	1996	—	—	—	—
Imbler	1997	1,016	10	May 26	May 23
LaCrosse	1997	983	20	May 23	May 23
Pendleton	1997	1,052	17	May 28	May 23
Pullman	1997	1,088	11	May 25	May 23
	1999	973	32	May 22	May 23
	2001	879	100	May 22	May 23
Hays, KS	1999	907	24	May 12	May 22
	2001	772	26	May 8	May 22
Sidney, NE	1999	777	12	June 3	June 7
	2001	896	62	June 6	June 7
Stillwater, OK	1999	1,287	21	May 7	May 1
	2001	1,240	21	May 11	May 1
Ft. Collins, CO	1999	848	27	May 29	May 31
Moscow, ID	1999	807	21	June 3	June 8
Moccasin, MT	1999	773	13	June 8	June 24
Havre, MT	1999	887	55	June 9	June 16
Bozeman, MT	1999	582	89	May 27	June 20

[a] Abbreviation: GDD, growing degree days.

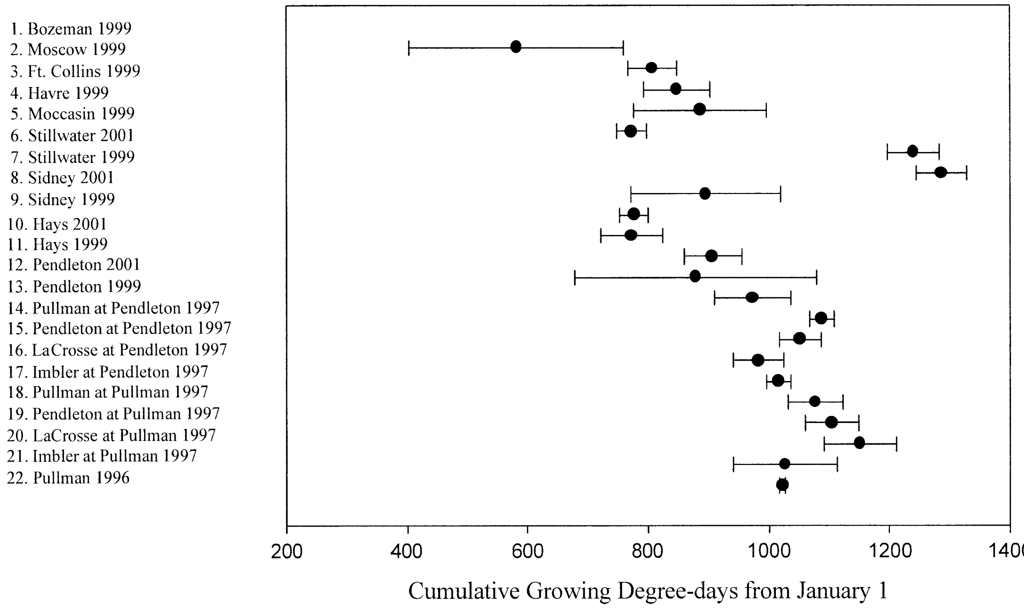

FIGURE 1. Estimated downy brome seed set for 10 locations in the western United States (± 2 SE).

of vernalization, biotype differences in vernalization requirement, or both. Whether the differences in biotype responses observed in these studies are a result of phenotypic or genetic factors is unknown. For these reasons, a universal assumption of a January 1 start date for cumulative GDD for all geographic locations is likely not valid.

Vernalization has been defined as the acquisition or acceleration of the ability to flower by a chilling treatment (Chouard 1960). Variation in the vernalization requirements and response seen in wheat may help explain differences observed between Bozeman and Stillwater downy brome seed-set GDD because there is a high degree of synteny among *Poaceae* genomes (Devos et al. 1995).

Cultivars of wheat and wheat from different geographical regions have differing sensitivities to vernalization temperatures (Kato and Yokoyama 1992; Manupeerapan et al. 1992; Slafer and Rawson 1995). Not only do temperatures at which vernalization will occur vary from 0 to 12 C (Brooking 1996), but the rate of vernalization changes with temperature (Brooking 1996; Hay and Ellis 1998; Trione and Metzger 1970). When vernalization requirements are met, vernalization is "saturated" (Fowler et al. 1996), and other processes may proceed. Research on duration of vernalization in winter annual grass weeds found that the longer the duration of vernalization, the shorter the time to maturity for ripgut brome (*Bromus diandrus* Roth) (Gleichsner and Appleby 1996) and jointed goatgrass (*Aegilops cylindrica* Host) (Walenta et al. 2002).

The change from vegetative to reproductive development in wheat is related to vernalization and leaf number (Brooking 1996). Under low-temperature vernalization, few leaves have emerged and few primordial leaves have formed when vernalization saturation causes primordial tissue to form the spike. However, under warm-temperature vernalization, several leaves have emerged and several primordial leaves have formed when vernalization saturation causes primordial tissue to form the spike. The spike emerges more quickly from the low-temperature wheat than from the warm-temperature wheat because fewer leaves in the surrounding whorl must emerge before the spike emerges (Brooking 1996).

The downy brome biotype by location interaction found in the biotypes study may be explained when the above information is taken into account. The performance of a biotype cannot be predicted when the biotype is put into a different thermal environment (Slafer and Rawson 1995) because biotype traits are different.

Western region results may be explained by looking at climate and vernalization temperatures. Downy brome at Bozeman, MT, was exposed to low temperatures in winter and spring and set seed with fewer GDD than other sites. It may be that because the optimum temperature for vernalization was low for this biotype, and the required duration of vernalization was met early in the year, primordial tissue changed to a reproductive spike early. Bozeman downy brome required few cumulative GDD to put out all its leaves and spike. The seed-set GDD calendar date, May 27, 1999, is as late as it is due to the rate of GDD accumulation at Bozeman. In contrast, downy brome at Stillwater, OK, was exposed to warm temperatures in winter and spring and set seed with more GDD than other sites. However, the calendar date of seed set was earlier than other sites. It may be that because the optimum temperature for vernalization was high for this biotype, and the required duration of vernalization was longer because of warmer temperatures, primordial tissue changed to a reproductive spike after more cumulative GDD. Stillwater downy brome may have had more vegetative development (i.e., more primordial leaves in the whorl) than Bozeman downy brome at the time of vernalization saturation and spike formation, but subsequent rapid accumulation of GDD and leaf emergence resulted in a calendar date of May 7, 1999, and May 11, 2001, for seed-set GDD.

The differences among biotypes at different locations and the wide range of seed-set GDD values from Bozeman (582 GDD) to Stillwater (1,287 GDD) may be accounted for, and possibly modeled, if different base temperatures (temperatures below which vegetative development ceases) were used for different biotypes. Additionally, different optimum vernalization temperatures or vernalization saturation requirements might require using different start dates for cumulative GDD at different geographic locations.

Results for Pendleton and Pullman from the three studies revealed downy brome populations that are similar in seed-set GDD. The thermal environment and vernalization traits of these brome populations must be similar. A GDD model for the region using 1,000 GDD as a decision guideline may provide a management tool for downy brome.

Using information presented here, Pacific Northwest growers can determine when operations to control downy brome need to be performed to prevent production of viable weed seed. Failure to obtain effective control before these cutoff dates (May 23 at Pendleton and June 11 at Pullman) will allow the perpetuation of downy brome infestations in subsequent winter wheat crops. Downy brome population response to GDD will need to be evaluated in other locations before suggesting a model for use by vegetation managers outside of the inland Pacific Northwest.

Sources of Materials

[1] Optic StowAway® Temperature logger, Onset Computer Corporation, P.O. Box 3450, Pocasset, MA 02559-3450.

Acknowledgments

The authors would like to thank A. J. Bussan, Drew Lyon, Tom Peeper, Phil Stahlman, Donn Thill, and Phil Westra for collecting downy brome samples and David Legg for statistical consultation.

Literature Cited

Ball, D. A. 1992. Weed seedbank response to tillage, herbicides, and crop rotation sequence. Weed Sci. 40:654–659.

Ball, D. A., B. Klepper, and D. J. Rydrych. 1995. Comparative above-ground development rates for several annual grass weeds and cereal grains. Weed Sci. 43:410–416.

Ball, D. A. and C. Mallory-Smith. 2000. Sulfonylurea herbicide resistance in downy brome. Pages 41–42 *in* Proceedings of the Western Society of Weed Science. Reno, Nevada: Weed Science Society of America.

Blackshaw, R. E. 1994. Rotation affects downy brome in winter wheat. Weed Technol. 8:728–732.

Brooking, I. R. 1996. Temperature response of vernalization in wheat: a developmental analysis. Ann. Bot. 78:507–512.

Chouard, P. 1960. Vernalization and its relations to dormancy. Annu. Rev. Plant Physiol. 11:191–237.

Daugovish, O., D. J. Lyon, and D. D. Baltensperger. 1999. Cropping systems to control winter annual grasses in winter wheat (*Triticum aestivum*). Weed Technol. 13:120–126.

Deen, W., L. A. Hunt, and C. J. Swanton. 1998. Photothermal time describes common ragweed (*Ambrosia artemisiifolia* L.) phonological development and growth. Weed Sci. 46:561–568.

Devos, K. M., G. Moore, and M. D. Gale. 1995. Conservation of marker synteny during evolution. Euphytica 85:367–372.

Dotray, P. A. and F. L. Young. 1993. Characterization of root and shoot development of jointed goatgrass (*Aegilops cylindrica*). Weed Sci. 41: 353–361.

Fowler, D. B., L. P. Chauvin, A. E. Limin, and F. Sarhan. 1996. The regulatory role of vernalization in the expression of low-temperature-induced genes in wheat and rye. Theor. Appl. Genet. 93:554–559.

Gleichsner, J. A. and A. P. Appleby. 1996. Effects of vernalization on flowering in ripgut brome (*Bromus diandrus*). Weed Sci. 44:57–62.

Hay, R.K.M. and R. P. Ellis. 1998. The control of flowering in wheat and barley: what recent advances in molecular genetics can reveal. Ann. Bot. 82:541–554.

Hay, R.K.M. and E.J.M. Kirby. 1991. Convergence and synchrony—a review of the coordination of development in wheat. Aust. J. Agric. Res. 42:661–700.

Kato, K. and H. Yokoyama. 1992. Geographical variation in heading characters among wheat landraces, *Triticum aestivum* L., and its implication for their adaptability. Theor. Appl. Genet. 84:259–265.

Klepper, B., R. K. Belford, and R. W. Rickman. 1984. Root and shoot development in winter wheat. Agron. J. 76:117–122.

Klepper, B., R. W. Rickman, and C. M. Peterson. 1982. Quantitative characterization of vegetative development in small cereal grains. Agron. J. 74:789–792.

Klepper, B., R. W. Rickman, J. F. Zuzel, and S. E. Waldman. 1988. Use of growing degree-days to project sample dates for cereal crops. Agron. J. 80:850–852.

Mallory-Smith, C., P. Hendrickson, and G. Mueller-Warrant. 1999. Cross-resistance of primisulfuron-resistant downy brome to sulfosulfuron. Weed Sci. 47:256–257.

Manupeerapan, T., J. L. Davidson, C. J. Pearson, and K. R. Christian. 1992. Differences in flowering responses of wheat to temperature and photoperiod. Aust. J. Agric. Res. 43:575–584.

Pacific Northwest Weed Management Handbook. 2002. Corvallis, OR: Oregon State University. 420 p.

SAS Institute Inc. 1989. SAS/STAT User's Guide. Version 6, 4th ed., Volume 2. Cary, NC: Statistical Analysis Systems Institute. 846 p.

Slafer, C. A. and H. M. Rawson. 1995. Base and optimum temperatures vary with genotype and stage of development in wheat. Plant Cell Environ. 18:671–679.

Thill, D. C., R. D. Schirman, and A. P. Appleby. 1980. Influence of afterripening temperature and endogenous rhythms on downy brome (*Bromus tectorum*) germination. Weed Sci. 28:321–323.

Trione, E. J. and R. J. Metzger. 1970. Wheat and barley vernalization in a precise temperature gradient. Crop Sci. 10:390–392.

Walenta, D. L., J. P. Yenish, F. L. Young, and D. A. Ball. 2002. Vernalization response of plants grown from spikelets of spring and fall cohorts of jointed goatgrass. Weed Sci. 50:461–465.

Wilen, C. A., J. S. Holt, and W. B. McClosky. 1996. Predicting yellow nutsedge (*Cyperus esculentus*) emergence using degree-day models. Weed Sci. 44:821–829.

Yenish, J. P., J. D. Doll, and D. D. Buhler. 1992. Effects of tillage on vertical distribution and viability of weed seed in soil. Weed Sci. 40: 429–433.

Received May 7, 2003, and approved October 8, 2003.