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Phenological Development of Spring Barley in a Short-Season Growing Area

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ABSTRACT

Understanding the phenological development of barley (*Hordeum vulgare* L.) grown under field conditions in its major growing area in the northern Great Plains, the Canadian province of Alberta, is important for the development of a crop model in this area. Five cultivars of barley registered for production on the Canadian Prairies were grown at three locations in Alberta (Botha, Lacombe, and Olds) from 1993 to 1996. Measurements and estimates were made of 12 growth stages, the final leaf number of the main culm, phyllochrons, and leaf area indices (LAIs). The average phyllochron was 69.1 growing degree days (GDD), and the final leaf number was 9.0. While location–year differences in GDD requirements to reach successive stages could be related to environmental conditions, the genotypic effects and genotype × environment (g × e) interactions would require that specific genotypic coefficients be introduced into the model. For instance, 'Manley' required only 129 GDD to emerge and 493 GDD to reach Apex 1 but required 1495 GDD to reach physiological maturity while 'Tukwa' required 133 GDD to emerge, 514 GDD to reach Apex 1, and only 1431 GDD to reach physiological maturity. Despite genotypic differences in reaching specific growth stages, all cultivars had very synchronous growth under the wide range of environments encountered in the 12 location-years of these tests. This should allow for the development of a crop model for barley that will accurately predict growth stages and the allocation of resources to the growth and maintenance of plant structures (leaves, stems, spikes, and kernels).

THE MAJOR GROWING AREA FOR BARLEY in North America is in the northern Great Plains where the Canadian province of Alberta produces approximately 6 Tg on 2 million ha (AAFRD, 1999). About 80% of the barley produced in Alberta supports its Can$3 billion livestock industry (CGC, 1996). Barley is also used for malt production and a small amount is used for human food. Understanding the development of barley in this environment is crucial to continued advancement in its breeding and to production systems and crop growth simulation models for this crop.

Phenology is the development of a plant through successive growth stages. It is important for understanding biomass partitioning and stress assessment. Several growth-staging systems have been developed for cereals and Landes and Porter (1989) compared 23 of them. Commonly-used scales to describe plant growth, such as BBCH (Lancashire et al., 1991) and that of Haun (1973), are based on the external appearance of the plant. Other scales, such as that of Banerjee and Wienhues [B&W] (1965), describe apical growth.

Although scales based on external appearance and apical growth can be very precise, the relationships between them are not always clear, and depending on why stages are being measured, the selection of an appropriate scale is important (Landes and Porter, 1989). As well, the relationship of scales to environmental factors, temperature, photoperiod, and time are not always well understood. However, Rickman and Klepper (1995) developed an elegantly simple model relating the phenological development of the apex with the external development of the plant and thermal time. They illustrated the full-season synchronous initiation and development of all vegetative and reproductive parts of the plant as a function of average temperature sums. However, it may be that a nonlinear relationship that accounts for temperature and daylength effects on growth, such as the beta function described by Jame et al. (1998), may better explain the relationship of growth to GDD.

The phyllochron is the interval, either on a calendar or thermal unit basis, between the emergence of successive

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Published in Agron. J. 93:370–379 (2001).

Abbreviations: B&W, Banerjee and Wienhues; g × e, genotype × environment interaction; GDD, growing degree days; LAI, leaf area index; LAI_{max}, maximum leaf area index.

leaves (Rickman and Klepper, 1995). For spring barley at a given temperature, the emergence of new leaves was found by Cao and Moss (1989a) to be a linear function of time, and differences in the rate of appearance were found between temperatures and genotypes. For spring barley as well, the emergence of new leaves at a given daylength was found by Cao and Moss (1989b) to be a linear function of time, and differences were observed between daylengths and genotypes. Cao and Moss (1989c) also pointed out that although phyllochrons for spring barley varied among genotypes and combinations of temperature and daylength, they increased as either temperature or daylength increased. Kirby (1995) reported that the rate of leaf appearance was set early in the life cycle. Frank and Bauer (1995) noted that the phyllochron has been widely accepted by crop modelers for predicting plant development and by producers for determining the timing of management practices such as irrigation, fertilizer, and pesticide applications.

Studies relating the morphological stages of barley to thermal time have been made in Alaska (Dofing, 1992; Dofing and Karlsson, 1993; Sharratt, 1999), Australia (López-Castañeda and Richards, 1994), North Dakota (Bauer et al., 1993), Quebec (Ma and Smith, 1992), Spain (Garcia del Moral et al., 1991), Syria (van Oosterom and Acevedo, 1992), and under growth room conditions (Frank and Bauer, 1997). Phyllochrons for spring barley have been determined in Alaska (Dofing and Karlsson, 1993; Sharratt, 1999), Alberta (Jedel and Helm, 1994b), North Dakota (Frank and Bauer, 1995), and Syria (van Oosterom and Acevedo, 1992). Leaf development rates in barley have been studied by Cao and Moss (1989a, 1989b). Final leaf numbers in barley have been determined in Alaska (Dofing, 1992), Alberta (Jedel and Helm, 1994a), Australia (López-Castañeda and Richards, 1994), Britain (Gallagher, 1979), North Dakota (Bauer et al., 1993), Quebec (Ma and Smith, 1992), and Syria (van Oosterom and Acevedo, 1992). Variation found in the literature of values (GDD) for phenological traits are, in part, due to differences in when the measurements started (sowing vs. emergence). As well, they may reflect location differences in temperatures and daylengths (Jame et al., 1998). As Cao and Moss (1986b) found that the phyllochron decreased as daylength increased, so the smaller phyllochrons found in Alaska vs. those in Syria could be explained on the basis of daylength differences. The variation found in the literature illustrates why it is important that data be collected specifically for the development and validation of a barley crop model in the environment where it will be used unless all of the variability can be accounted for by coefficients and equations.

The objective of the research reported in this paper was to study the phenological development of several barley cultivars grown under field conditions. These data, in conjunction with biomass data that will be reported later, were used to develop and validate a crop model for barley (SPARC-Barley, developed by Y. Jame), especially for use in the Alberta portion of the Great Plains.

MATERIALS AND METHODS

These tests were conducted from 1993 to 1996 at Botha [Daysland loam, 60% orthic Black Solod (coarse loamy, Typic Argiustoll with a natric horizon) and 40% thin orthic Black Chernozem (coarse loamy, frigid Typic Haplustoll)], Lacombe [Penhold loam, orthic Black Chernozem (coarse loamy, frigid Typic Haplustoll)], and Olds [Didsbury loam, orthic Black Chernozem (coarse loamy, frigid Typic Haplustoll)]. These soils are considered nutrient rich due to their high organic matter contents of 7 to 13% and high N levels before seeding (NO_3 levels before seeding ranging from 32–111 mg kg^{-1} and NH_4 levels ranging from 8–39 mg kg^{-1} in the top 0–15 cm of soil).

Plot size from 1993 to 1995 was eight 6.10-m-long rows with 0.14-m row spacing. Plots were trimmed to six 2.74-m-long rows with 0.14-m row spacing before final harvest. Plot size in 1996 at all three sites was eight 4.57-m-long rows with 0.14-m row spacing. Plots were twinned, two plots of the same treatment, so that biomass samples over the growing season were taken from one plot and LAIs, phenological stages, and the yield at final harvest were taken from the adjacent plot. Plots were trimmed to six 2.52-m-long rows with 0.14-m row spacing before final harvest.

Plots were seeded using a belt-type seeder in 1993 on 11 May at Botha, 14 May at Lacombe, and 12 May at Olds; in 1994 on 9 May at Botha, 5 May at Lacombe, and 12 May at Olds; in 1995 on 9 May at Botha, 9 May at Lacombe, and 11 May at Olds; and in 1996 on 21 May at Botha, 13 May at Lacombe, and 17 May at Olds. Seeds were treated with 2 mL kg^{-1} Vitavax single solution [a.i. carbathiin (5,6-dihydro-2-methyl-*N*-phenyl-1,4-oxathiin-3-carboxamide)]. The seeding rate was approximately 200 seeds m^{-2} based on kernel weights. The seeding depth was approximately 0.04 m.

Fertilizer applications were based on soil tests done in the fall of the year previous to seeding; 112 kg ha^{-1} of a premix blend of ammonium phosphate ($NH_4H_2PO_4$) and potassium chloride (KCL) was incorporated with the seed. Weeds were controlled by hand weeding and the application of herbicides. In 1993 at Lacombe, Lorsban [a.i. chlorpyrifos (*O*,*O*-diethyl *O*-(3,5,6-trichloro-2-pyridinyl) phosphorothioate)] was applied at 1200 mL ha^{-1} to control cutworms.

The five barley cultivars used in these tests were 'Brier', 'Duel', Manley, Tukwa and 'Seebe'. Brier, Duel, and Tukwa are six-row cultivars while Manley and Seebe are two-row cultivars. Duel and Manley are malt types while the others are classed as feeds. Tukwa and Duel mature 1 d earlier than the cultivar Harrington while Brier is similar maturing and Manley and Seebe mature 3 to 4 d later (AAFRD, 1997). Brier, Duel, and Seebe are tall cultivars at 83, 90, and 84 cm, respectively, while Manley is a standard-height cultivar at 78 cm and Tukwa is a semidwarf cultivar at 72 cm (AAFRD, 1997). Seebe has good resistance to scald [*Rhyncosporium secalis* (Oud.) J. Davis], which is generally the most prevalent leaf disease in Alberta, while Brier and Tukwa have intermediate resistance and Duel and Manley are susceptible (AAFRD, 1997). Tukwa and Brier have intermediate resistance to the spot form of net blotch (*Pyrenophora teres* f. *maculata* Drechs.), also a common leaf disease in Alberta, while the other three cultivars are susceptible (AAFRD, 1997).

Weather Measurements

Weather data were collected from on-site weather stations located within 2 km of the plots. Minimum, maximum, and mean temperatures were collected daily along with solar radiation and precipitation data using a LI-1000 DataLogger (LI-COR, Lincoln, NE) at all location-years except Olds in 1993 when a Campbell system [Campbell Scientific (Canada) Corp. Edmonton, AB] was used. When data were missing, missing values were replaced by data obtained from Agriculture and Agri-Food Canada for the Lacombe site (approximately 3 km from the site); Olds College for the Olds site (approximately 5 km from the site); and the Conservation and Development Branch of Alberta Agriculture, Food, and Rural Development for the Botha site (approximately 25 km from the site). Growing Degree Days were calculated as the accumulation of daily mean temperatures

$$\sum(T_m > 0°C) \quad [1]$$

where T_m is the mean temperature. When T_m was unavailable, but the maximum and minimum temperatures were available, GDD was calculated as

$$\sum[(T_{max} + T_{min})/2 > 0°C] \quad [2]$$

where T_{max} is the maximum temperature and T_{min} is the minimum temperature.

Soil Measurements

In 1993 and 1994, soils were sampled in the fall previous to planting to determine nutrient status. Before seeding and after harvest in 1994, soils were sampled using a hand corer to determine moisture content to depths of 30 or 45 cm. Soil nutrient analyses were done by Norwest Labs, Edmonton, AB.

In 1995 and 1996, deep soil core samples were collected before seeding and after harvest to depths of 0.9 to 1.5 m. Deep core samples were analyzed for moisture, N, and bulk densities. Organic matter, sand, silt, and clay content were determined on a selected subsample. Phosphorous, K, pH, and electroconductivity were determined for the 0- to 15-cm depth. Soil nutrient analyses were done by Soil and Crop Diagnostic Centre, Edmonton, AB.

Plant Measurements

Phenological stages were monitored throughout the growing season and based on 50% of the plot at each stage: emergence (the first true leaf visible, BBCH 10); Apex 1 (the first node 0.01 m or above the soil surface, BBCH 30); flag leaf emerged (the ligules of the flag leaf visible, BBCH 39); flag leaf fully elongated (fully elongated flag leaf, no BBCH stage); anthesis (the central florets of the head having shed their pollen, BBCH 61); heading (heads fully emerged from the leaf sheath of the flag leaf, BBCH 55); peduncle fully elongated (the last internode or peduncle fully elongated, no BBCH stage); milk (kernels with milky endosperms, BBCH 75); soft dough (kernels with soft, doughy endosperms, BBCH 85); physiological maturity (loss of green color from the peduncle, corresponding to approximately 30% kernel moisture content, BBCH 87). Emergence was determined as GDD from sowing while all other stages were determined as GDD from emergence.

To assess early development, dissections were made in 1994 and 1995 to determine the apical development of the main culm. Stages were assigned according to the scale of B&W (1965). Leaf numbers were counted on the main culm before dissections.

Leaf counts based on the Haun (1973) scale were made once a week from emergence to flag leaf on the main culm. Five plants were selected per plot by tagging shortly after emergence. Using fine multicolored wire, tillers were distinguished from the main culm. We marked the fifth leaf of the main culm by cutting approximately 1 cm from the end of the leaf to give a blunt end that was easily visible as the stem elongated and lower leaves senesced. These data were regressed against GDD, and the slope was taken as the phyllochron in GDD. Final leaf numbers were determined as the number of leaves on the main culm. Leaf areas were measured three to five times throughout the growing season using a LI-COR LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, NE). Due to lodging at Olds in 1995, LAIs could not be measured using this method.

Statistical Analysis

The experimental design was a randomized complete block with five cultivars and four replicates at each location. Analyses were conducted using PROC GLM of SAS (SAS Inst., 1988). Locations and cultivars were treated as fixed effects while years and times of measurements were treated as random effects. Errors appropriate to mixed models were used to test for the significance of the effects (Steel and Torrie, 1980). Phyllochrons were determined as the slope of the linear equations of weekly leaf numbers regressed against GDD accumulated since emergence using PROC GLM of SAS (SAS Inst., 1988). For the B&W data, stage was regressed as a linear function of GDD from emergence to sampling date using PROC GLM. Leaf numbers at sampling for B&W staging were also regressed against GDD at sampling to predict the leaf number at double ridge (B&W 4) and glume initials (B&W 7). Quadratic equations were fitted to the LAI data by year, location, and cultivar to determine maximum LAI (LAI_{max}) and time of LAI_{max} in GDD.

RESULTS AND DISCUSSION

The Environments

Accumulated precipitation during the growing season was highest at Olds in 1993, 1995, and 1996 with initial soil moisture contents of 0.366 and 0.287 kg kg^{-1} in 1995 and 1996, respectively (initial soil moisture not determined in 1993). However, in 1994, Olds had the lowest accumulated precipitation (Fig. 1) and a low initial soil moisture content of 0.151 kg kg^{-1} for the top 0 to 15 cm. Accumulated precipitation for Botha and Lacombe were very similar in 1994 and 1995 (Fig. 1). While Botha had a low initial soil moisture content in 1994 (0.179 kg kg^{-1} for the top 0–15 cm), initial soil moisture content at Lacombe was higher (0.246 kg kg^{-1} for the top 0–15 cm). In 1995, initial soil moisture contents were good at both locations (0.279 kg kg^{-1} at Botha and 0.387 kg kg^{-1} at Lacombe). Lacombe had higher accumulated precipitation in 1993 and lower accumulated precipitation than Botha in 1996 (Fig. 1). However, both locations had good initial soil moisture contents in 1996 (0.301 kg kg^{-1} at Botha and 0.283 kg kg^{-1} at Lacombe). The long-term average precipitation (May–Sept.) is 303 mm for Botha, 311 mm for Lacombe, and 335 mm for Olds (Jedel and Salmon, 1993). While 1993 and 1995 were near-average years at Olds, 1994 and 1996 were dry. At Botha and Lacombe in all 4 yr, rainfall was below average.

Mean daily temperatures during the growing season remained >0°C and <25°C at all locations (Fig. 2), which is well within the growing range for barley (Jame et al., 1998). The only exception was a cold period in early May 1996. Temperature patterns within years were very similar at the three locations, except at Botha in 1993. Temperatures were slightly higher at Botha and lower at Olds compared with Lacombe, reflecting the

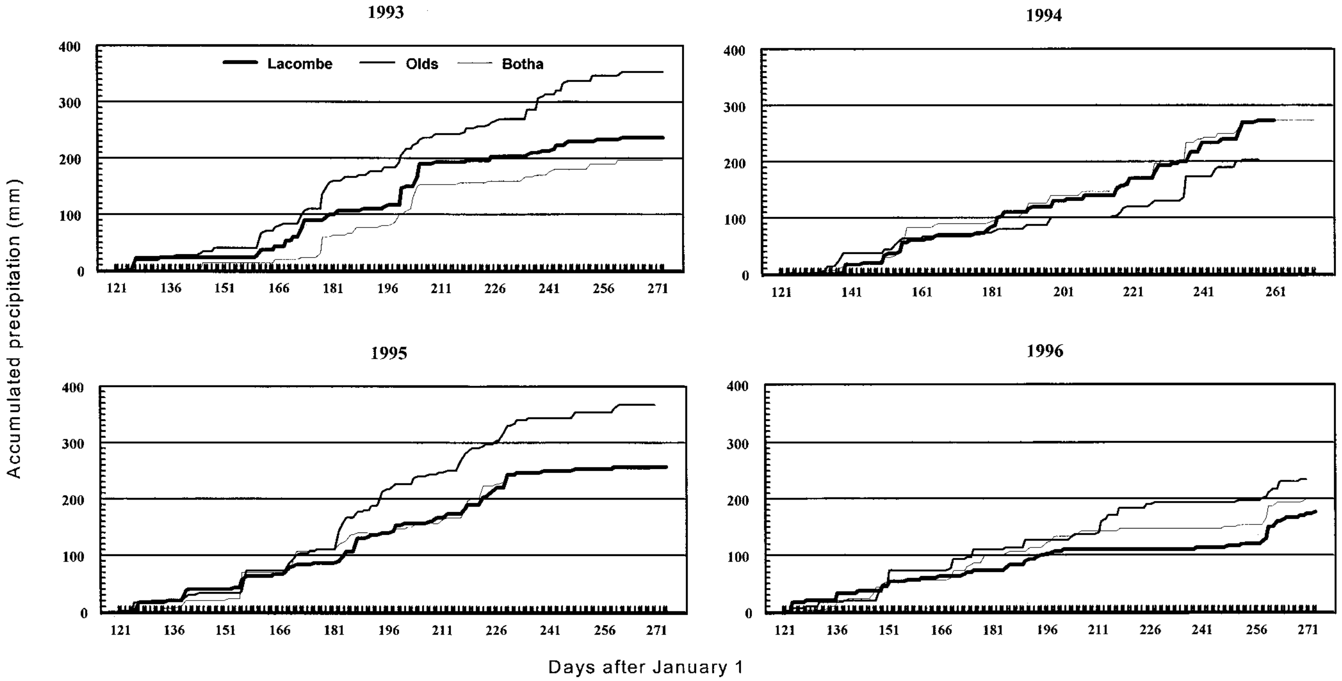

Fig. 1. Total precipitation (mm) from sowing at three locations in Alberta, Canada (Botha, Lacombe, and Olds) in 1993, 1994, 1995, and 1996.

long-term averages from May to September of 13.7°C at Botha, 12.9°C at Lacombe, and 12.5°C at Olds (Jedel and Salmon, 1993).

Plant Growth

Emergence

The year × location × cultivar interaction effect for emergence was significant (Table 1). The range in GDD from sowing to emergence of 91 to 192 in the environments studied (Table 2) was greater than the 63 GDD reported by Bauer et al. (1993) for spring barley grown in North Dakota, but it does encompass the 125 GDD reported by Kirby (1995) for barley grown in Britain. The relationship of emergence to genotypic and environmental effects was complex, being influenced by the soil moisture availability at seeding, precipitation after seeding, soil and air temperatures, and genotype. While

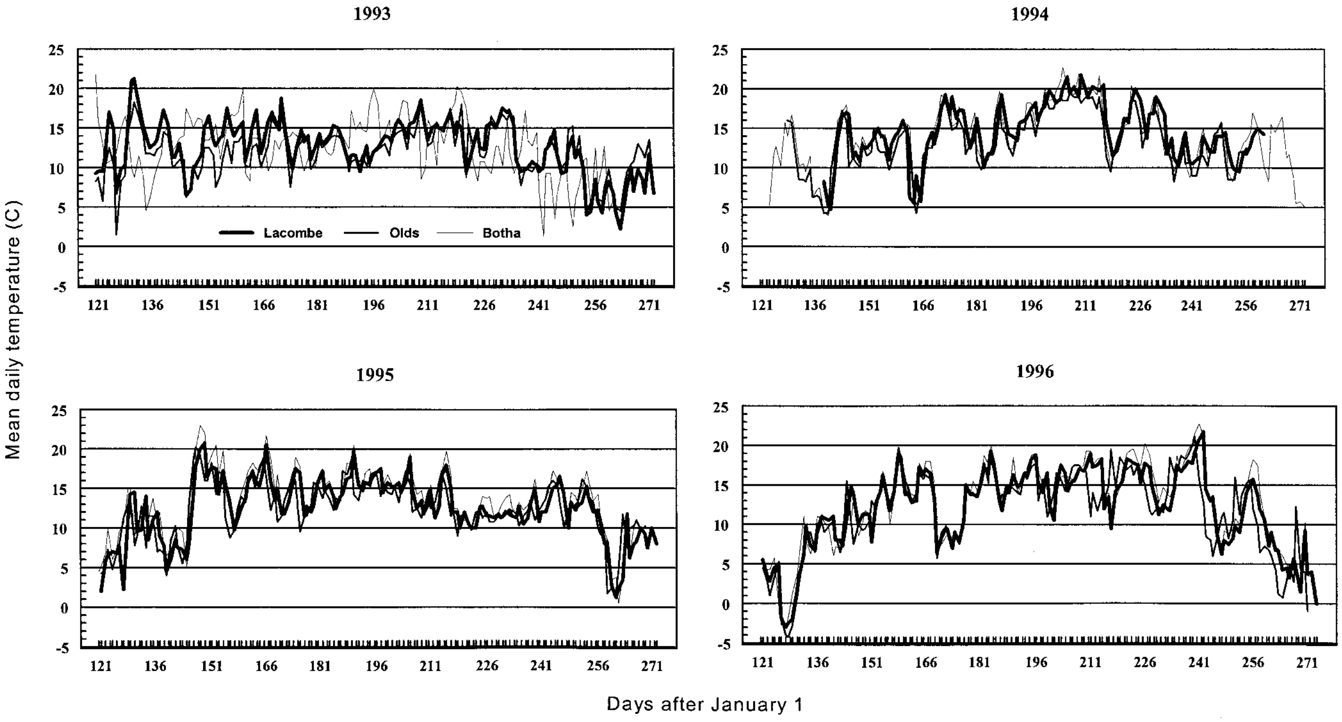

Fig. 2. Mean daily temperature (°C) from sowing at three locations in Alberta, Canada (Botha, Lacombe, and Olds) in 1993, 1994, 1995, and 1996.

Table 1. Mean squares (MS) from the analysis of variance for growing degree days (GDD) from sowing to emergence and from emergence to nine phenological stages of five barley cultivars grown from 1993 to 1996 at three locations in Alberta, Canada (Botha, Lacombe, and Olds).

Source of variation	df	Emergence†	Apex 1	Flag leaf emerged	Anthesis	Heads fully emerged	Kernels at soft dough
Year (y)	3	5 247.92 (ns)	28 081.9 (ns)	9 219.3 (ns)	47 245.1 (ns)	286 572.8**	84 101.6 (ns)
Location (1)	2	426.50 (ns)	120 418.8*	69 520.9 (ns)	112 679.2 (ns)	239 969.2*	217 218.1**
y × 1	6	2 347.50**	20 529.3**	23 492.0**	27 023.7**	28 535.1**	19 184.4**
Error a	36	296.90	512.1	275.2	330.4	277.5	621.0
Cultivar (c)	4	259.22 (ns)	3 123.1*	11 528.3**	21 657.3**	38 834.0**	12 547.0**
y × c	12	446.99**	818.3*	618.7 (ns)	1 327.9*	1 312.8 (ns)	484.7 (ns)
l × c	8	192.09 (ns)	442.5 (ns)	255.2 (ns)	644.6 (ns)	856.7 (ns)	235.5 (ns)
y × l × c	24	127.24*	347.4 (ns)	287.4 (ns)	495.6**	859.1**	602.1**
Error b	144	78.1	256.3	196.0	149.8	145.4	245.8

Source of variation	df	Flag leaf fully elongated	df	Peduncle fully elongated	Kernels at milk	df	Physiological maturity
Year (y)	1	43 455.8 (ns)	2	138 642.1 (ns)	50 602.4 (ns)	3	269 172.2 (ns)
Location (l)	2	103 301.5 (ns)	2	203 864.5 (ns)	248 651.6*	2	60 753.5 (ns)
y × l	2	16 451.2**	4	67 679.9**	15 971.4**	4	43 146.6**
Error a	18	172.6	27	1 979.5	326.0	30	1 370.0
Cultivar (c)	4	13 462.2**	4	43 252.4**	6 384.0**	4	22 979.7**
y × c	4	414.7 (ns)	8	2 700.8 (ns)	434.1 (ns)	12	3 281.4 (ns)
l × c	8	337.9 (ns)	8	4 135.7 (ns)	495.0 (ns)	8	2 228.4 (ns)
y × l × c	8	219.2 (ns)	16	2 400.3*	537.2*	16	1 472.2**
Error b	72	158.1	108	1 193.3	266.5	120	479.4

* Significant at the 0.05 level.

** Significant at the 0.01 level.

† Where year was tested by [MS(y × l) + MS(y × c) − MS(y × l × c)]; y × l was tested by [MS(error a) + MS(y × l × c) − error b]; and other effects were tested by errors appropriate to a mixed model.

the malt types may have been expected to have faster emergence than the feed types—as rapid, uniform germination is a desirable trait in the malt house—no differences in emergence were found in the six-row cultivars (Table 3). For the two-row cultivars, Manley, the malt type, was earlier than Seebe in 8 of 12 location-years (significantly so in four, data not shown) while Seebe was significantly earlier than Manley in two. It is this type of g × e interaction that a crop model must be able to predict. While emergence may have been expected to be most rapid in the warm, moist soils of 1995, it was in fact most rapid in the cool, moist soils of 1996 (data not shown).

Apical Growth Stages

In the current study, the B&W growth stages were found to be a linear function of GDD for barley (Table 4), which is consistent with the model of Rickman and Klepper (1995). As the highest-order significant interaction was for year × cultivars (Table 5), only these linear relationships were determined (Table 4). In the 2 yr in which B&W growth stages were assessed, there was little difference between cultivars, with higher slopes in 1994 than 1995, suggesting more rapid development in 1994 vs. 1995 (Table 4). The low initial soil moistures in 1994 may have stimulated the apex to initiate successive stages of apical development earlier. The late cultivar, Manley, tended to have fewer GDD requirements to reach double ridge than the other cultivars while the other late cultivar, Seebe, had the greatest GDD requirement (Table 4). These results are contrary to the results of Garcia del Moral et al. (1991), who found that the days to double ridge were fewer in early maturing cultivars than in cultivars of medium maturity for spring barley grown in Spain. They also indicate the importance of determining the genotypic coefficients for all growth stages rather than relying on only late stages.

Table 2. Means, range, and standard error (SE) for phenological stages, phyllochrons, and final leaf number of five barley cultivars grown from 1993 to 1996 at three locations in Alberta, Canada (Botha, Lacombe, and Olds).

Trait	Mean	SE	Range Min.	Range Max.
	GDD (0° C base)			
Sowing to emergence	133	1.1	91	192
Emergence to:				
Apex 1	505	3.1	410	601
Flag leaf emerged	681	2.7	565	809
Flag leaf fully elongated	755	5.0	648	864
Anthesis	813	3.4	705	966
Heading	916	5.5	756	1109
Peduncle fully elongated	991	6.6	827	1204
Kernels at milk	1036	4.8	913	1169
Kernels at soft dough	1242	4.0	1126	1387
Physiological maturity	1455	6.2	1268	1702
Phyllochron	69.1	0.74	42.6	107.5
Final leaf number	9.0	0.02	6.0	11.0

Average GDD to double ridge was 158, ranging from 123 to 184 (Table 4); this was fewer than the 215 GDD found by Bauer et al. (1993) for barley grown in North Dakota. The greater GDD required in 1994 did not appear to be due to warm weather although under controlled conditions, Frank and Bauer (1997) found that barley required more GDD to reach double ridge under hot (26°C) conditions than cool (18°C) conditions. Average GDD to glume initials was 312, ranging from 273 to 369 (Table 4). This range reflects the findings of Frank and Bauer (1997) for barley grown under cool (18°C) conditions.

During the time from double ridge to glume initials, spikelet number is being set. Environmental factors during this time will affect this yield component. Therefore, stresses such as those due to herbicide application,

Table 3. Cultivar differences in growing degree days (GDD) from sowing to emergence and from emergence to nine phenological stages, phyllochron intervals, and final leaf number averaged over three locations in Alberta, Canada (Botha, Lacombe, and Olds) and 4 yr (1993–1996).

Cultivar	Designation†	Sowing to emergence	GDD from emergence to: Apex 1	Flag leaf emergence	Flag leaf fully elongated‡	Anthesis	Heads fully emerged
		GDD					
Brier	6R,F,Mi,T	134.3	503	667	735	789	886
Duel	6R,M,E,T	135.3	508	672	747	810	897
Manley	2R,M,L,S	129.2	493	696	781	835	953
Seebe	2R,F,L,T	133.2	509	699	779	834	938
Tukwa	6R,F,E,Sd	133.4	514	669	732	796	903
LSD$_{0.05}$		9.4	12.7	12.5	16.3	16.2	16.1

Cultivar	Designation†	GDD from emergence to: Peduncle fully elongated§	Kernels at milk§	Kernels at soft dough	Physiological maturity¶	Phyllochron	Final leaf no.
		GDD				GDD leaf^{-1}	no.
Brier	6R,F,Mi,T	959	1030	1230	1440	66.3	9.2
Duel	6R,M,E,T	959	1028	1233	1440	65.6	9.1
Manley	2R,M,L,S	1031	1049	1263	1495	74.9	8.8
Seebe	2R,F,L,T	1024	1051	1256	1470	71.1	9.2
Tukwa	6R,F,E,Sd	983	1021	1228	1431	67.7	9.0
LSD$_{0.05}$		28.2	11.3	9.8	25.5	2.33	0.20

† 6R, six-rowed; 2R, two-rowed; F, feed; M, malt; E, early; Mi, mid maturity; L, late; T, tall; S, standard height; Sd, semidwarf from Alberta Agriculture, Food, and Rural Development (1997).

‡ Data from 1995 and 1996 only.

§ Data from 1994, 1995, and 1996 only.

¶ Data missing from Lacombe, 1993, and Olds, 1995.

drought, or frost during this period may adversely affect yield due to effects on spikelet number and viability (ovary and anther development). Leaf numbers were estimated to range from 2.8 to 4.2 during the stage from double ridge to glume initials (Table 4), a time coincident with herbicide application. Jedel and Helm (1994b) had reported earlier that double ridge occurred at the two- to three-leaf stage for a different group of spring barley cultivars grown in Alberta.

Apex 1

At this stage, internode elongation has pushed the apical meristem above the soil surface. Before this stage, resources allocated to the growth of aboveground structures are going to leaf and apical development while after this stage, resources are split between leaf, apical, and stem development. Location, year × location, cultivar, and year × cultivar effects on this trait were significant (Table 1). Manley remained the earliest cultivar attaining this stage, having the lowest GDD requirement from emergence to Apex 1 while Tukwa had the greatest GDD requirements to reach Apex 1 (Table 3). The range in GDD from emergence to Apex 1 was from 410 to 601 (Table 2), which was slightly longer than the 405 GDD reported by Bauer et al. (1993) for barley grown in North Dakota.

Flag Leaf Emergence

The flag leaf is the last leaf to emerge, and once it is fully elongated, resources allocated to the growth of aboveground structures will go only to completing stem elongation and apical development. At the flag leaf emergence stage, the last leaf of the main culm was now visible. While Brier and Duel had greater GDD requirements to emerge than the other cultivars and Tukwa had a greater GDD requirement to reach Apex

Table 4. Banerjee and Wienhues (B&W) growth stages for spring barley as a linear function of growing degree days (GDD) (Stage = $a + \beta \times$ GDD) when grown for 2 yr in central Alberta (avg. over three locations). Estimations of GDD to double ridge (B&W growth stage 4) and glume initials (B&W growth stage 7) based on linear functions; and leaf number based on GDD estimations at these two stages.

Year	Cultivar	Intercept (a)	β	r^2***	GDD to double ridge	GDD to glume initials	Leaf number at double ridge	Leaf number at glume initials
1994	Brier	−1.670	0.031	0.91	183	280	3.02	4.35
	Duel	−1.516	0.031	0.91	178	275	2.47	3.88
	Manley	−1.188	0.030	0.94	173	273	2.91	4.24
	Seebe	−1.216	0.029	0.91	180	283	2.83	4.26
	Tukwa	−1.902	0.032	0.93	184	278	2.59	3.90
1995	Brier	1.808	0.015	0.49	146	346	3.01	4.55
	Duel	1.835	0.015	0.47	144	344	2.63	4.19
	Manley	2.022	0.015	0.50	132	332	3.11	4.43
	Seebe	2.197	0.013	0.42	142	369	2.93	4.52
	Tukwa	2.285	0.014	0.45	123	337	2.52	4.12
Overall means		–	–	–	158	312	2.80	4.24

*** Significant at the 0.001 level.

Table 5. Mean squares (MS) from the analysis of variance for Banerjee & Wienhues (B&W) stages, final leaf number, and phyllochron for five barley cultivars grown from 1993 to 1996 at three locations in Alberta, Canada (Botha, Lacombe, and Olds).

Source of variation	df	B&W stage†	df	Phyllochron interval‡	df	Final leaf number§
Year (y)	1	471.387 (ns)	3	130.37 (ns)	3	5.53 (ns)
Location (l)	2	97.099 (ns)	2	4544.73 (ns)	2	1.73 (ns)
y × l	2	93.218**	6	2550.66**	6	7.70**
Error a	18	2.680	36	22.98	36	0.45
Cultivar (c)	4	20.488 (ns)	4	716.66**	4	5.80**
y × c	4	7.357*	12	27.42 (ns)	12	1.01 (ns)
l × c	8	2.349 (ns)	8	35.74 (ns)	8	0.60 (ns)
y × l × c	8	1.108 (ns)	24	32.73**	24	0.54**
Error b	72	1.580	144	9.48	144	0.28
Plant	4	1.930 (ns)	–	–	235	0.24 (ns)
Error c	2776	10.901	–	–	718	0.21

* Significant at the 0.05 level.

** Significant at the 0.01 level.

† Where year was tested by [0.9988 × MS(y × l) + MS(y × c) − 0.9988 × MS(y × l × c)]; y × l was tested by [0.9812 × MS(error a) + MS(y × l × c) − 0.9812 × error b]; y × c was tested by [0.9988 × MS(y × l × c) + (0.0012 × MS(error b)]; y × l × c was tested by [0.9812 × MS(error b) + 0.0188 × MS(error c)]; and other effects were tested by errors appropriate to a mixed model.

‡ Where year was tested by [MS(y × l) + MS(y × c) − MS(y × l × c)]; y × l was tested by [MS(error a) + MS(y × l × c) − error b]; and other effects were tested by errors appropriate to a mixed model.

§ Where year was tested by [0.9998 × MS(y × l) + 0.9998 MS(y × c) − 0.9997 MS(y × l × c)]; location was tested by [0.9997 × MS(y × l) + 0.0003 × MS(error c)]; y × l was tested by [0.9924 × MS(error a) + 0.9998 × MS(y × l × c) − 0.9913 × error b]; cultivar was tested by [0.9999 × MS(y × c) + 1.31 × 10^{-6} × MS(y × l × c) + 0.0001 MS(error c)]; y × c was tested by [0.9999 × MS(y × l × c) + 0.0001 × MS(error c)]; l × c was tested by [0.9998 × MS(y × l × c) + 0.0002 × MS(error c)]; y × l × c was tested by [0.9915 × MS(error b) + 0.0085 × MS(error c)]; and other effects were tested by errors appropriate to a mixed model.

1, these three cultivars were the earliest to reach flag leaf emergence (Table 3). Both Manley and Seebe were late in reaching flag leaf emergence. While the year × location effect was significant, there was no significant g × e interaction. Therefore, this trait should be easier to predict than other traits were g × e was present (Table 1).

Flag Leaf Fully Elongated

When the flag leaf is fully elongated, resources allocated to the growth of aboveground structures no longer need to be partitioned to leaf growth. The six-row cultivars had a lower GDD requirement to reach this stage than the two-row cultivars (Table 3). The range in GDD from emergence to flag leaf fully elongated was from 646 to 864 (Table 2), which was longer than the 528 GDD reported by Bauer et al. (1993) for barley grown in North Dakota. As for flag leaf emergence, no g × e effects were noted for this trait.

Anthesis

Anthesis in barley generally occurs while the spike is still in the boot—usually only one-fourth to three-fourths of the spike is emerged. At this stage, apical development has been completed. Resources allocated to aboveground structures will now go to completing stem elongation and kernel formation. Stem elongation will often cease when stresses occur during this stage, as kernel fill seems to have precedence, and spikes may not completely emerge from the boot. While the year × location × cultivar interaction effect for GDD to anthesis was significant (Table 1), Brier required markedly less GDD to reach anthesis than all of the other cultivars except Tukwa (Table 3) in all environments (data not shown). Manley and Seebe, the two-row cultivars, had the greatest GDD requirements to reach anthesis (Table 3). Duel had the greatest GDD requirement to move from flag leaf fully elongated to anthesis. Jedel and Helm (1994a) also found that days to anthesis were longer for two-rowed cultivars than for six-rowed cultivars. The range in GDD from emergence to anthesis was from 705 to 966, which was greater than the 669 GDD reported by Bauer et al. (1993) for barley grown in North Dakota.

Heads Fully Emerged

When heads do not fully emerge from the boot, stresses may be occurring that are delaying or stopping the completion of stem elongation. However, even in the drought years (Fig. 1), these cultivars tended to have complete head emergence. This trait was complexly influenced by years, locations, and cultivars (Table 1) and so may be difficult to predict. The six-row cultivars generally had a lower GDD requirement to complete head emergence than the two-row cultivars (Table 3). Seebe was late but had a significantly lower GDD to complete heading than Manley in 4 of 12 location-years (data not shown). Seebe may have been more stress-tolerant than Manley, and therefore was able to complete head emergence earlier. The range in GDD from emergence to heads fully emerged was from 756 to 1109 with an average of 916 (Table 2), which was slightly greater than the average of 834 found by Bauer et al. (1993) for spring barley grown in North Dakota.

Peduncle Fully Elongated

Full elongation of the peduncle marks the completion of stem elongation. After this stage, resources allocated to aboveground structures will be going to maintenance and kernel fill. This trait was significantly affected by the interaction of year × location × genotype (Table 1), so it may be difficult to predict. The six-row cultivars had a lower GDD requirement to reach peduncle fully elongated than the two-row cultivars (Table 3).

Kernels at Milk Stage

From anthesis to milk stage, the kernels are in their lag phase of development as the cellular and structural components of the embryo and endosperm are being laid down. At the milk stage, the kernels begin to rapidly increase in size as starch is accumulated. While the six-row cultivars had a lower GDD requirement to reach milk than the two-row cultivars (Table 3), this was a complex trait with significant g × e effects (Table 1).

Kernels at Soft Dough Stage

Soft dough is a very important stage in barley when it is going to be used for greenfeed or be ensiled. The prediction of this stage to optimize quality and biomass is important to producers. The six-row cultivars had similar GDD requirements to reach soft dough while the two-row cultivars had greater requirements (Table 3). This was a complex trait with significant g × e effects (Table 1).

Physiological Maturity

At physiological maturity, remobilization of resources to the head for kernel fill has been completed. The two-row cultivars had the greatest GDD requirements to reach physiological maturity (Table 3). Manley and Seebe are known to be late-maturing cultivars, and therefore are not representative of all two-row barley cultivars in their phenological development. Jedel and Helm (1994a) found that two-rowed cultivars had similar days to physiological maturity as six-rowed cultivars. The range in GDD from emergence to physiological maturity was 1268 to 1702 (Table 2), which was greater than the 976 to 1200 GDD reported by Sharratt (1999) for barley grown in Alaska but less than the 1642 to 1925 GDD reported by López-Castañeda and Richards (1994) for barley grown in Australia.

Leaf Growth

Phyllochrons

The phyllochron is prone to error because temperature and daylength are known to affect the leaf appearance rate. Jame et al. (1998) have proposed a beta function to better estimate the leaf appearance rate. However, all of the linear regressions of the leaf number as a function of GDD for our tests were significant ($P < 0.001$) with r^2 values >0.90. The good fit to a linear model was due, in part, to the long days (>16 h) at all locations during leaf growth that would be near the peak of the daylength response found by Jame et al. (1998).

Brier and Duel had the lowest GDD requirement, or the shortest phyllochrons (Table 3). Therefore, although these cultivars emerged after Manley, they required fewer heat units to complete their life cycle. Manley had the longest phyllochron, which was significantly greater than that of Seebe (Table 3). So although Manley initiated leaf development earlier as indicated by GDD to emergence and Apex 1, it ended up being the latest-maturing cultivar studied due to greater GDD requirements for leaf development. However, if the phyllochrons are calculated from the data for the B&W samplings (Table 4), Manley had one of the shorter phyllochrons during this early period of growth. This variability in phyllochrons would support the use of the nonlinear technique of Jame et al. (1998) for the determination of leaf appearance rates. Long phyllochrons for two-row cultivars is not the norm; Frank and Bauer (1995) found that the two-rowed cultivar Bowman had the shortest phyllochron of the cultivars they studied.

Average phyllochron was 69.1 GDD with a range of 43 to 108 (Table 2), which was longer than the mean of 64.5 GDD found by Dofing and Karlsson (1993) for barley grown in Alaska and shorter than the mean of 77.2 GDD found by Frank and Bauer (1995) for barley grown in North Dakota. The range was greater than the range of 60 to 80 GDD found by Sharratt (1999) for barley grown in Alaska or the range of 88 to 104 GDD found by van Oosterom and Acevedo (1992) for barley grown in Syria.

The time from sowing to emergence was about two phyllochrons, which would be consistent with one phyllochron for the development of the coleoptile and one phyllochron for the first true leaf. Again, the early emergence of Manley would not be in relationship to its phyllochron based on the whole season, but it would be consistent with its phyllochron based on early season growth as indicated by the B&W samplings.

Final Leaf Number

Manley had the lowest final leaf number (Table 3), which is consistent with earlier initiation of double ridge (Table 4). Although the location × year × cultivar effect was significant (Table 1), variability for final leaf number within a location-year-cultivar was relatively small (data not shown). The final leaf number of the main culm of barley in these tests was 9.0 when averaged over years, locations, and cultivars (Table 2). While cultivar differences were observed, none were significantly different than the mean of 9.0 (Table 3). This final leaf number is similar to those reported by Gallagher (1979) for barley grown in Britain and to those reported by Ma and Smith (1992) for barley grown in Quebec. It is higher than the reports of Dofing (1992) and Dofing and Karlson (1993) for barley grown in Alaska, Jedel and Helm (1994b) for barley grown in Alberta, López-Castañeda and Richards (1994) for barley grown in Australia, and Bauer et al. (1993) for barley grown in North Dakota. However this final leaf number is less than that reported by van Oosterom and Acevedo (1992) for barley grown in Syria. The semidwarf Tukwa had a similar leaf number to the other cultivars (Table 3), so although Tukwa was early maturing, this early maturity was not due to a reduction in leaf number or a short phyllochron; instead, it must have been due to accelerated postanthesis growth. The GDD required to reach flag leaf emergence (mean 681) was slightly more than that required to produce 9.0 leaves with an average phyllochron of 69 GDD leaf^{-1}. These types of disparities

Table 6. Maximum leaf area indices (LAI_{max}) and time of LAI_{max} as a function of growing degree days (GDD) for five barley cultivars grown at three locations for 4 yr.†

		LAI_{max}						GDD to LAI_{max}					
Year	**Location**	**Brier**	**Duel**	**Manley**	**Seebe**	**Tukwa**	**Mean**	**Brier**	**Duel**	**Manley**	**Seebe**	**Tukwa**	**Mean**
1993	Botha	5.76‡	5.55	5.89	6.29	5.80	5.86§	1069¶	1060	1091	1086	1101	1081#
	Lacombe	4.73	5.16	5.00	5.04	5.04	4.99	765	910	928	784	869	851
	Olds	5.23	5.27	6.04	6.38	6.14	5.81	1025	1022	1059	1065	1045	1043
1994	Botha	3.89	3.25	3.21	3.75	3.74	3.57	1056	1081	1151	1075	1071	1087
	Lacombe	4.88	4.07*	6.09	5.21	5.65	5.18	1073	1149	1170	1159	1112	1133
	Olds	5.00	4.77	5.32	5.25	5.05	5.08	937	975	1036	1014	996	992
1995	Botha	5.34	5.24	5.42	6.07	5.47	5.51	1174	1097	1123	1196	1114	1141
	Lacombe	5.44	5.66	5.89	5.59	5.90	5.70	1081	1120	1175	1128	1125	1126
1996	Botha	5.07	4.79*	5.24	5.82	5.28	5.24	1049	1058	1081	1062	1059	1062
	Lacombe	6.06	5.61	6.02	6.16	5.77	5.92	1021	1017	1026	1023	1017	1021
	Olds	5.96	5.97	5.95	6.36	6.39	6.13	891	927	939	950	931	928
Cultivar mean		5.21††	5.03	5.46	5.63	5.48		1013‡‡	1038	1071	1049	1040	

*** Quadratic equation not significant at $P \leq 0.05$.**
† Unable to calculate quadratic equations for LAI vs. GDD at Olds, 1995.
‡ For the comparison of cultivar LAI_{max} means between and within location-years, LSD(0.05) = 0.30.
§ For the comparison of location-year LAI_{max} means, LSD(0.05) = 0.419.
¶ For the comparison of cultivar GDD to LAI_{max} means between and within location-years, LSD(0.05) = 82.7.
 # For the comparison of location-year GDD to LAI_{max} means, LSD(0.05) = 37.0.
†† For the comparison of cultivar LAI_{max} means, LSD(0.05) = 0.221.
‡‡ For the comparison of cultivar GDD to LAI_{max} means, LSD(0.05) = 27.3.

must be accounted for in a crop model, and they support a nonlinear relationship between the leaf appearance rate and GDD as proposed by Jame et al. (1998).

Leaf Area Indices

Once the leaves and stems are fully elongated, LAI would be expected to be maximized. The estimations of LAI_{max} on a GDD basis were later than peduncle fully elongated and usually occurred near the milk stage (Tables 3 and 6). This lateness may be due to the development of secondary tillers lagging behind the main culm. As well, the demand for carbohydrates concurrent with kernel fill causes remobilization demands that result in senescence. The prediction of LAI_{max} is important for green-feed and silage production because there is a loss of leaf material that is important to the quality of these feeds after this time. As for other traits, LAI_{max} usually occurred earlier in Brier, Duel, and Tukwa than in Seebe or Manley (Table 6). The predicted range in LAI_{max} from 3.21 to 6.39 depended on location and cultivar. Under Australian conditions, LAI_{max} for barley was found to be 5.3 by López-Castañeda and Richards (1994). For barley, LAI_{max} occurred at about 900 GDD under Australian conditions, while under Alberta conditions, we found it occurred at about 1040 GDD. The semidwarf Tukwa had a similar LAI_{max} to the other cultivars, as would be expected because it had similar leaf numbers. Despite its lower leaf number, Manley had a higher LAI_{max} than Duel or Brier. The production of secondary tillers, which is higher in two-row cultivars than in six-row cultivars (Jedel and Helm, 1994a), must compensate for low main culm leaf numbers.

CONCLUSION

The five cultivars evaluated in this test represented a wide range of spring barley types grown in western Canada—early to late maturing, malt or feed, two- or six-rowed, semidwarf to tall. In the group tested, there was a late-maturing cultivar with rapid initial growth (Manley); a late-maturing cultivar with slow growth throughout its life cycle (Seebe); an early cultivar with slow initial growth (Tukwa); and midmaturing cultivars with slow initial growth. Although one of the cultivars studied, Duel, had been classified as early, in these tests, it had the same maturity as the midmaturing cultivar, Brier. While genotype and environmental differences were found, the barley plant shows a remarkable synchrony of development under a wide range of conditions. However, a crop model for barley needs to address cultivar differences in development rates and environmental response.

As well, the barley crop model needs to address the complexity of kernel development occurring concurrently with the completion of stem elongation and the differences among cultivars in their ability to complete stem elongation under stress conditions. Use of the phyllochrons determined in this study for a crop model could be erroneous if the relationship of leaf count to GDD was not linear, and estimation of LAI_{max} could be inaccurate if the relationship of LAI to GDD was not quadratic (nonsignificant regressions noted in Table 6). The relationship of GDD to flag leaf emergence and full elongation were the only traits where g × e effects were not evident, so these stages should be easier to incorporate into the model than more complex traits where g × e was evident. The data collected can be used to relate stages to GDD, leaf number, and apical development.

The year × location interaction was significant for all of the traits measured, underscoring the importance of site-specific data for model development. Each environment offered a complex setting of different temperatures, radiation, precipitation, and soil conditions. As well, there were different stress conditions from location-year to location-year for which the model would have to be able to predict cultivar responses.

The purpose of measuring or calculating of 12 growth stages and the phyllochron was to develop a model for barley that can accurately predict the stages of importance for the distribution of biomass for growth and maintenance. The model must accurately predict across a wide range of environmental conditions for the cultivar being grown for producers to accept using crop models to time harvest and applications of pesticides, fertilizers, and irrigation water. These data collected for the development and validation of a crop growth model help us to understand more fully the phenological development of the barley crop in the Alberta portion of the Great Plains.

ACKNOWLEDGMENTS

Our thanks to Alberta Agricultural Research Institute, Alberta Barley Commission, Agrium, and Soil and Crop Diagnostic Centre for their financial assistance in support of this research. For their technical support, we gratefully acknowledge Dave Dyson, Donna Westling, and Tom Zatorski at Field Crop Development Centre; Jason Liick and Wayne Thick at SPARC; and Karen Cannon at the Agronomy Unit.

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