AN ABSTRACT OF THE DISSERTATION OF

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Title: Vernalization Requirements and Seed Dormancy of Jointed Goatgrass (*Aegilops cylindrica*).

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Jointed goatgrass (*Aegilops cylindrica* Host) infestations in winter wheat (*Triticum aestivum* L.) production regions of the central and western USA result in severe economic losses in the wheat market. Field and greenhouse studies were conducted to determine the vernalization requirements of winter wheat, spring wheat, jointed goatgrass, and wheat by jointed goatgrass reciprocal hybrid plants. In field studies, jointed goatgrass plants required more vernalization to produce spikelets and germinable seed than 'Madsen' winter wheat plants. In greenhouse studies, plants of jointed goatgrass populations collected from Oregon and Washington wheat fields required fewer vernalization days to reach the joint stage than Madsen plants. Detailed observations in the greenhouse revealed a longer period between jointing and anthesis for most jointed goatgrass populations that was overlooked in field studies. Vernalization for 6-wk represents the minimum treatment for synchronous reproductive development among jointed goatgrass populations, Madsen winter wheat, and Madsen by jointed goatgrass hybrids, yet the risk of gene transfer might be greater after 7-wk vernalization. In the jointed goatgrass populations tested, there was not selection for a vernalization insensitive growth habit. Because jointed goatgrass spikelets often contain two seed, germination was recorded for primary and secondary positioned seed. Germination of freshly harvested jointed goatgrass seed was promoted by 25/15 C day/night temperatures. However, light and 30/20 C incubation was necessary for maximum germination of non-dormant, primary positioned seed. Both primary and secondary positioned seed within jointed goatgrass spikelets were non-dormant after 16-wk after-ripening at 22 ± 2 C. Under optimum growing conditions, no planting depth selectively allowed wheat germination and emergence while preventing jointed goatgrass germination and emergence. Glume removal did not alleviate dormancy completely in jointed goatgrass seed. Research confirmed jointed goatgrass population polymorphism for vernalization requirements and seed dormancy. Jointed goatgrass reproductive variability might be part of a general purpose genotype strategy to germinate and colonize a wide range of environments. Wheat by jointed goatgrass hybrid plants should be removed from winter and spring wheat fields. Despite a short dormancy period, three or more years of rotation outside of winter annual crops may be necessary to reduce populations of jointed goatgrass.

Vernalization Requirements and Seed Dormancy of Jointed Goatgrass (*Aegilops cylindrica*)

by

Lynn Fandrich

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I understand that my dissertation will become a part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Lynn Fandrich, Author

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CONTRIBUTION OF AUTHORS

Dr. Robert Zemetra provided direction in the design and organization of the field and greenhouse vernalization experiments.

Jennifer Hansen created the wheat by jointed goatgrass reciprocal hybrid plant materials.

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Vernalization Requirements and Seed Dormancy of Jointed Goatgrass (*Aegilops cylindrica*)

CHAPTER 1

General Introduction

Jointed goatgrass (*Aegilops cylindrica* Host; $2n = 4x = 28$; CCDD genomes) infestations in winter wheat (*Triticum aestivum* L.; $2n = 6x = 42$; AABBDD genomes) production regions of the central and western USA result in $145 million annual losses in the wheat market (Anonymous 2004). Because jointed goatgrass and wheat are genetically related, and their life histories are similar (Ball et al. 1995; Miller 1995; Dotray and Young 1988; Fenster and Wicks 1976; Johnston and Parker 1929), strategies for jointed goatgrass control have been limited to cultural practices, crop rotation, and tillage. Recently, selective control of jointed goatgrass in winter wheat became possible through the release of herbicide-resistant wheat cultivars (Haley et al. 2003; Lazar et al. 2003). However, the possible transfer of a herbicide-resistance gene from winter wheat to jointed goatgrass poses a threat to the success of this program. To assess the risk of gene movement from herbicide-resistant winter wheat to jointed goatgrass, information about the reproductive development of winter wheat, jointed goatgrass, and wheat by jointed goatgrass hybrid plants is required. Integrated management practices specific to several winter wheat production regions have been recommended also for jointed goatgrass control (Evans et al. 1999; Pester et al. 1999; Young et al. 2002). Detailed study of jointed goatgrass seed dormancy in response to environmental and genetic influences might be used to improve the effectiveness of integrated weed-management strategies.

A herbicide-resistance gene might introgress into a jointed goatgrass population due to the sexual compatibility between wheat and jointed goatgrass (Seefeldt et al. 1998; Snyder et al. 2000; Zemetra et al. 1998). The potential for recombination and gene exchange between wheat and jointed goatgrass exists because of homologous D genome chromosome pairing (Kimber and Zhou 1983; Riley and Law 1965; Zemetra et al. 1998).

The transfer of a herbicide-resistance gene into jointed goatgrass via a hybrid bridge, followed by backcrossing and restoration of self-fertility, might lead to the persistence of a herbicide-resistance gene in a jointed goatgrass population. Breaking the gene flow process at the hybrid bridge is one management approach to prevent gene movement from winter wheat to jointed goatgrass. Quantification of winter wheat and jointed goatgrass vernalization requirements is necessary to predict the conditions under which jointed goatgrass plants can establish and be available for crossing with wheat.

Vernalization is defined as the effect of chilling that corresponds to accelerated reproductive development (Chouard 1960). Exposure to low temperatures for several weeks allows plants to escape the risks of cold injury during reproductive growth (Flood and Halloran 1986), and synchronizes cereal development in response to long photoperiods (Hay and Kirby 1991; Hay and Ellis 1998). In the absence of vernalization, the vegetative period is extended, and floral initiation is delayed (Richardson et al. 1986). Winter wheat plants require approximately 4-6 wk vernalization at temperatures below 10 C to induce flowering and are planted in the fall. Spring wheat plants are vernalization insensitive and flower without such a treatment. The timing of wheat flowering may be determined by the interactions of three sets of genes: 1) vernalization (*Vrn*); 2) photoperiod (*Ppd*) genes that act in response to cold and day length; and 3) earliness per se (*Eps*) genes that act independently of the environment to determine the number of vegetative and floral primordia initiated (Snape et al. 2001).

Numerous studies have quantified the developmental responses of wheat to vernalization and photoperiod, but the context of its vernalization response compared to its weedy relative, jointed goatgrass, remains relatively unknown. Synchronous development among winter wheat, jointed goatgrass, and hybrid plants at the anthesis stage after exposure to varied vernalization conditions would increase the potential for herbicide-resistance gene migration and persistence in jointed goatgrass populations. Hybrid infestations have been observed also in Oregon spring wheat and spring barley fields during surveys conducted from 1998-2000 (Morrison et al. 2002a), in 2001 (personal observation), and by other researchers (Walenta et al. 2002). Migration of the dominant *Vrn-1* vernalization insensitive allele (Brule-Babel and Fowler 1988) from spring wheat to jointed goatgrass might lead to the development of spring type jointed goatgrass populations, rendering a spring cropping regime ineffective for jointed goatgrass control.

Dormancy is an important characteristic for propagation of weed species that reproduce by seed (Baker 1974). Studies on jointed goatgrass seed production and dormancy are few and only a limited number of populations have been investigated. The jointed goatgrass spike has 3-11 spikelets arranged alternately along a main stem. Each spikelet produces two to five florets (Hitchcock 1950; Johnston and Parker 1929; McGregor 1987), and seed are produced most often in the two lowest positioned florets (primary and secondary). Seed from jointed goatgrass are produced and shed in early to mid-summer, and are exposed immediately to hot soil surface temperatures and limited soil moisture. Survival of a germinated seed through these conditions is unlikely. The presence of dormancy delays germination until autumn when optimum temperatures and adequate moisture for germination and growth are available.

Temperature is a major environmental factor that affects the persistence of dormancy in temperate grasses and influences germination after seed imbibe water (Simpson 1990). Mature seed may germinate to 100% at all temperatures (non-dormant), between 0 and 100% at low but not at high temperatures (thermally dormant), or not at any temperature (dormant). As dormant and partially dormant seed after-ripen, germination occurs over a broader range of temperatures such that narrow, specific requirements for germination are lost (Vegis 1964). Gleichsner (1987) reported that jointed goatgrass was under the control of thermal dormancy, i.e., more seed germinated at low rather than high temperatures, but the experiment was not repeated, and alternating temperature regimes were not tested. Morrow et al. (1982) reported that seed of freshly harvested jointed goatgrass spikelets germinated at 10, 15, and 20 C, but not at higher temperatures. Additional research should be conducted on jointed goatgrass seed germination to expand on the results of Gleichsner (1987) and Morrow et al. (1982). An understanding of jointed goatgrass seed dormancy would be improved through experiments that incorporate alternating incubation temperatures and include seed from several jointed goatgrass populations.

Hot and dry conditions experienced by jointed goatgrass seed lying on the soil surface might alleviate seed dormancy over time through a process described as after-ripening (AR) - the interaction between seed and environment over time that leads to dormancy loss (Simpson 1990). Quantification of jointed goatgrass seed AR requirements provides a description of time and environment necessary to relieve completely dormancy in jointed goatgrass seed. However, current literature fails to accurately describe the effect of AR on jointed goatgrass seed. Gleichsner reported that jointed goatgrass seed gained the ability to respond to a wider range of temperatures over a 0.5 to 12 month period (1987), but additional results were not published. Morrow et al. (1982) observed that more 1 yr old seed germinated at temperatures ranging from 10 to 35 C than did freshly harvested seed, but shorter AR time periods were not tested. Further research on the effect of AR on jointed goatgrass seed germination is warranted. Control measures designed to remove germinated seedlings will be most effective when the majority of seed in the seed bank are non-dormant.

Exposure to light breaks dormancy in many weed species, but there are species in which light has no effect or inhibits germination. Baskin and Baskin (1998a) summarized that among 54 grass species, germination of 28 was promoted by light, 13 were unaffected by light or dark conditions, and 13 were inhibited by light. The effect of light on germination of jointed goatgrass seed is unclear. Cleary and Peeper (1980) reported in field studies that more jointed goatgrass spikes were produced on plants that established on the soil surface than plants that emerged from 5 or 16 cm. Jointed goatgrass infestations were more frequent also in areas where producers have adopted conservation tillage (Schweitzer et al. 1988), possibly because more spikelets are left on the soil surface compared to conventional tillage. Because light has been shown to be a significant germination factor for many weed species (Bewley and Black 1994), cultivation at night has been to used successfully reduce the germination of weeds in newly established crops (Hartmann and Nezadal 1990; Klaffke 1998).

Jointed goatgrass seed germination might be a function of AR and germination environments, and also under the influence of spikelet structures surrounding the seed. The potential for spikelet structure influence on jointed goatgrass seed germination exists because of its flowering biology. The inflorescence in jointed goatgrass is composed of spikelets arranged compactly and alternately along the main axis of the spike (Hitchcock 1950; Johnston and Parker 1929; McGregor 1987), and the dispersal unit of jointed goatgrass is a spikelet. The lemma and the palea adhere tightly to jointed goatgrass seed, and the florets remain attached to the glumes (Heyne 1950; Johnston and Parker 1929). The lemma and palea in wild oat (*Avena fatua* L.) contain germination inhibitors (Chen et al. 1982), and limit gas exchange to and from the caryopsis (Hay and Cumming 1959). The physical influence of the glumes, lemma, and palea on jointed goatgrass seed germination is not known.

Spikelet position on the spike, combined with the effects of environment during seed maturation and the age of the plant at seed development, accounts for a great deal of the variability among weed populations known to exhibit large variations in germination (Andersson and Milberg 1998). Donald and Zimdahl (1987) examined seed production in two Colorado jointed goatgrass populations and reported that approximately 20% of spikelets had one seed, 80% had two seed, and less than 1% had three seed. However, they did not clarify seed production by floret or spikelet position on the spike. Carpenter and Thill (1992) reported that primary positioned seed from the middle of the spike were more dormant than primary seed from the upper and lower spike regions, but further results were not published. Efforts to model the life history of jointed goatgrass and predict germination should be adjusted to account for spikelet position on the spike, and floret position within the spikelet.

The objectives of the studies described herein were to evaluate the relative vernalization requirements of jointed goatgrass, winter wheat, spring wheat, and wheat by jointed goatgrass reciprocal hybrid plants, and to characterize dormancy in freshly harvested jointed goatgrass seed. Relative vernalization requirements of jointed goatgrass, winter wheat, and spring wheat were determined by field experiments at three Oregon locations, while quantification of the phenology and reproductive development of all plants in response to varying vernalization conditions was determined in the greenhouse. Specific dormancy parameters included in the investigations were 1) incubation temperature; 2) the AR period; 3) light and dark incubation environments; 4) spikelet structures; and 5) spikelet position within the spike and floret position within the spikelet. Several jointed goatgrass populations of Oregon and Washington origin were included in the investigations. Wheat cultivars grown commonly in the Pacific Northwest were used as comparative standards.

CHAPTER 2

Vernalization Responses of Field Grown Jointed Goatgrass, Winter Wheat, and Spring Wheat

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Numerous studies have quantified the developmental responses of wheat to vernalization and photoperiod, but the context of its vernalization response compared to its weedy relative, jointed goatgrass, remains relatively unknown. Six paired jointed goatgrass populations collected from Washington and Oregon fields and winter and spring wheat were grown in field studies to quantify yield, reproductive tiller production, and germination in response to vernalization. Monthly planting dates initiated in October and concluded in March were used to vary the vernalization durations for plants sown at three Oregon locations over two growing seasons. Jointed goatgrass plants required more vernalization to produce spikelets and germinable seed than winter wheat plants. Spring wheat plants were unaffected by vernalization. A minimum of 48 vernalization days (Mar 3 planting) at Pendleton in 2002-03 were required for jointed goatgrass plants to produce germinable seed, and plants that were exposed to 34 vernalization days (Mar 24) failed to head in the same summer. Winter wheat planted at Pendleton on Mar 24 produced seed that germinated to 100%. Once minimum vernalization thresholds were met, jointed goatgrass and winter wheat yields responded similarly to increasing vernalization days. The effects of vernalization on jointed goatgrass yields, reproductive tiller production, and seed germination percentages were more pronounced at Pendleton and Moro, OR, locations where jointed goatgrass has adapted, compared to Corvallis, OR, where it has not adapted. Jointed goatgrass populations varied in vernalization response. Plants from populations that originated at The Dalles remained vegetative when exposed to 57 vernalization days (Feb 24), while plants of Bickleton and Helix origin headed. There has not been selection for spring adapted jointed goatgrass populations in the populations tested. Yet if spring temperatures were cool, minimum conditions for vernalization may be satisfied, and the benefits of planting spring crops to control jointed goatgrass would be reduced.

Nomenclature: jointed goatgrass, *Aegilops cylindrica* Host, AEGCY; winter wheat, *Triticum aestivum* L. Madsen; spring wheat, *Triticum aestivum* L., Penawawa.

Key words: germination, growing degree days, reproductive tillers, vernalization days, yield.

Propagation of an annual plant species requires the production of a sufficient number of viable seed. The transition from a vegetative to a reproductive stage requires proper timing to ensure moisture and nutrients reach fertilized ovules to produce these seed. Temperatures must be in the optimal range for development and growth. Freezing temperatures cause cells to rupture and die, while hot temperatures shorten floral development and decrease pollen viability (Copeland and McDonald 2001). Plant development and the transition to flowering have been studied in numerous species. In winter annuals, which germinate in the fall and reproduce in early summer of the following year, a vernalization requirement prevents plants from entering the reproductive growth stage until the risk of low temperature stress has passed (Flood and Halloran 1986). The vernalization requirement is met through prolonged exposure to cold temperatures, and winter annual plants then respond rapidly to stimuli that initiate flowering (Chouard 1960). In the absence of vernalization, the vegetative period is longer, and floral initiation is delayed (Richardson et al. 1986) such that vegetative plants may not survive the summer drought (Baskin and Baskin 1974).

Numerous studies have quantified the developmental responses of wheat (*Triticum aestivum* L.) to vernalization and photoperiod, but the context of its vernalization response compared to its weedy relative, jointed goatgrass (*Aegilops cylindrica* Host), remains relatively unknown. The timing of wheat flowering may be determined by the interactions of three sets of genes: 1) vernalization (*Vrn*); 2) photoperiod (*Ppd*) genes that act in response to cold and day length; and 3) earliness per se (*Eps*) genes that act independently of the environment to determine the number of vegetative and floral primordia initiated (Snape et al. 2001). Jointed goatgrass is described as a winter annual species (Hitchcock 1950). It has a quantitative vernalization requirement that must be met before it will flower and produce seed within a growing season (Donald 1984).

Jointed goatgrass was introduced into the United States in the late 19th century (Johnston and Heyne 1960), has since spread rapidly over 3 million ha (Anonymous 2002), and is now associated with multi-million dollar costs in the wheat industry (Ogg 1993). Because jointed goatgrass and wheat growth and development are similar (Dotray and Young 1988; Fenster and Wicks 1976; Johnston and Parker 1929), strategies for control of jointed goatgrass are limited traditionally to cultural practices, crop rotation, tillage, and more recently, the use of herbicide-resistant wheat (Haley et al. 2003; Lazar et al. 2003). Among the recommendations for cultural control of jointed goatgrass is to plant spring crops (Veseth 1988). Spring tillage and planting usually destroy established jointed goatgrass seedlings. In theory, newly emerged spring jointed goatgrass plants are not exposed to sufficient cold temperatures to satisfy vernalization requirements and flower before wheat harvest, fall tillage, or herbicide application. Observations of jointed goatgrass reproducing in spring cropped fields mandates testing for the selection of spring adapted or vernalization insensitive jointed goatgrass populations. Furthermore, weedy species may be polymorphic in flowering ability; a trait that contributes to successful adaptations in varied and stressed environments. Because of this genetic variability, winter and spring types could result through selection in winter and spring cropping systems.

The objective of this study was to evaluate the relative vernalization requirements of jointed goatgrass, winter wheat, and spring wheat plants.

Materials and Methods

Mature spikelets of six jointed goatgrass populations were collected in 2001 from a roadside, and winter and spring wheat fields in north central and eastern Oregon, and south central Washington. ‘Winter’ jointed goatgrass populations originated from traditional winter wheat/fallow fields, while ‘spring’ populations were collected within fields with at least 5 yr continuous spring cropping. Spikes were clipped from the plants when the culms appeared dry – at or near the time of winter wheat harvest. Samples were returned to Corvallis, OR, spikes were broken apart, and spikelets were hand-cleaned to remove culms and debris. Samples were stored dry at room temperature (22 ± 2 C) until use. Certified seed from winter wheat ‘Madsen’ (Allan et al. 1989) and spring wheat ‘Penawawa’ were included in these studies.

The six populations of jointed goatgrass, winter wheat, and spring wheat were grown during the 2002-03 and 2003-04 field seasons at the Lewis Brown Horticultural

Farm, Corvallis, OR, at the Sherman County Experiment Station, Moro, OR, and at the Columbia Basin Agricultural Research Center, Pendleton, OR. Jointed goatgrass populations were planted side by side in paired rows according to site of origin (Table 2.1). Winter and spring wheat were planted as a pair. Jointed goatgrass spikelets and wheat seed were sown in three replicates of a randomized complete block design with replications as blocks. The experiment was repeated.

Table 2.1. Descriptions of jointed goatgrass habitat, elevation, and location for populations collected in 2001 and used in these studies.

		Elevation	Latitude	Longitude
Population	Habitat/type	---- m ----	---- ° N ----	---- ° W ----
Bickleton, WA – R	Roadside/unknown	920	46.00	120.30
Bickleton, WA – W	Crop/winter	920	46.00	120.30
The Dalles, OR – S	Crop/spring	58	45.60	121.18
The Dalles, OR – W	Crop/winter	62	45.70	120.73
Helix, OR – S	Crop/spring	535	45.85	118.65
Helix, OR – W	Crop/winter	535	45.85	118.65

Field sites were selected from areas without previous jointed goatgrass infestations. Sites were prepared in the fall for conventional winter wheat planting, and jointed goatgrass spikelets and winter and spring wheat seed (n=45) were sown 3 cm deep into 2 m rows spaced 60 cm apart. Thirty g of slow-release, granular fertilizer[1] were evenly spread down each furrow at planting. Spikelets and seed were sown at monthly intervals beginning in October and concluding in March (Tables 2.2 and 2.3). Sites were hand-weeded as necessary. Spring plantings at the Corvallis site were hand-watered in 2003 to aid germination, and all plantings at the Moro site received a single application of 2.24 kg ai/ha bromoxynil, 2.24 kg ai/ha MCPA, 21 g ai/ha thifensulfuron-methyl, and 10 g ai/ha tribenuron-methyl to control broadleaf weeds on April 8, 2004.

Observations on growth and development were recorded throughout the growing season on days coincident with the next planting. Near the time of winter wheat harvest appropriate to each location, plants were measured and hand-harvested. Row height, row length, and plants per row were recorded. To measure yields, a 50 cm quadrant was placed within an area representative of each row, reproductive tillers and plants were counted, and spikes were clipped and placed in paper bags. A representative section of spikes outside the 50 cm was harvested by row for germination studies. Yield samples were oven dried for 3 d at 70 C or until no further change in weight was recorded. Jointed goatgrass spikelets and wheat seed were cleaned and weighed; yields were measured to the nearest 0.01 g.

Table 2.2. Significant dates, growing degree days (GDD), and vernalization days (VD) accumulated by plants grown at Corvallis, Moro, and Pendleton, OR, for the 2002-03 growing season.

	Corvallis			Moro			Pendleton		
	Date	GDD	VD	Date	GDD	VD	Date	GDD	VD
Planting 1	Oct 8	2747	164	¥			Oct 17	2631	131
Planting 2	Nov 10	2416	145	Nov 17	1990	122	Nov 21	2377	111
Planting 3	Dec 14	2172	118	Dec 10	1928	114	Dec 28	2244	93
Planting 4	Jan 17	1868	89	¥			Jan 28	2110	74
Planting 5	Feb 24	1688	57	Mar 3	1645	60	Mar 3	1960	48
Planting 6	Apr 9	1308	24	Mar 24	1485	43	Mar 24	1760	34
End of vernalization	31-May-03			31-May-03			31-May-03		
Harvest	8-Jul-03			14-Jul-03			16-Jul-03		

¥ Planting was not possible due to poor field conditions.

Table 2.3. Significant dates, growing degree days (GDD), and vernalization days (VD) accumulated by plants grown at Corvallis, Moro, and Pendleton, OR, for the 2003-04 growing season.

	Corvallis			Moro			Pendleton		
	Date	GDD	VD	Date	GDD	VD	Date	GDD	VD
Planting 1	Oct 15	2731	149	Oct 21	2259	117	Oct 20	2663	116
Planting 2	Nov 12	2436	125	Nov 18	2109	103	Nov 17	2476	102
Planting 3	Dec 15	2200	107	Dec 17	2030	84	Dec 16	2351	81
Planting 4	Jan 22	2087	78	¥			Jan 28	2298	66
Planting 5	Feb 28	1851	44	Feb 23	1948	60	Feb 24	2188	44
Planting 6	Mar 29	1569	23	Mar 18	1786	39	Mar 18	1997	27
End of vernalization	31-May-04			31-May-04			31-May-04		
Harvest	14-Jul-04			22-Jul-04			20-Jul-04		

¥ Planting was not possible due to poor field conditions.

Concurrently, germination samples were stored at room temperature (22 ± 2 C) near low speed fans to minimize jointed goatgrass spikelet and wheat seed degradation from excess natural moisture. Samples of 25 or 50 spikelets or seed were used in the germination studies. Spikelets or seed from each population and location were placed on two 10.2 by 10.2 cm germination blotters[2] moistened with 25 ml deionized water in clear, covered, acrylic germination boxes[3]. Boxes were placed randomly in growth chambers set to 25/15 C and 12-h photoperiod. Additional water was added as needed. Germination counts were made 7 and 14 d after imbibition, and germination was defined as the presence of 3 mm radicle. Each germination experiment had two replicates, and the experiment was repeated.

Growing Degree Day and Vernalization Day Calculations

Daily weather data for the three field locations over two years were obtained from weather stations nearest the research sites. Growing degree days (GDD) were calculated based on a base temperature of 0 C subtracted from the daily average air temperature (C). Daily mean temperatures less than 0 C were assigned a zero heat unit value. Accumulated GDDs were calculated as the sum of daily heat values from planting until harvest.

Vernalization days were used to standardize sowing dates across locations and years. Daily GDD values from planting until May 31 were multiplied by effectiveness factors described in the CERES wheat development model by Ritchie et al. (1998) and used also by Baloch et al. (2003). Vernalization days were calculated only on GDD ranges between 0 and 15 C, and ranges between 3 and 6 C were assigned the greatest vernalization effectiveness. Weather records for the 30 yr average suggested that no vernalization was expected to occur at Corvallis after May 31 (Baloch et al. 2003). Corvallis weather data for 2002-04 confirmed that temperatures did not drop below 15 C after May 31. Temperature patterns were similar for Moro and Pendleton.

Data Analysis

Correlation coefficients among the agronomic characteristics (yield, reproductive tillers, and percent germination) were calculated using PROC CORR in SAS[4]. Agronomic characteristics plotted against vernalization days showed positive, linear relationships, and suggested that differences among populations, locations, and years might exist. Square root transformations of agronomic characteristics plus 1.00 were used to stabilize variance across populations, locations, and years. Linear regression using PROC MIXED was used to test the main and interaction effects of population, location, and year with vernalization days. Preliminary analyses showed an interaction between location, year, and vernalization days. Data were analyzed with the independent regressions of each agronomic characteristic against vernalization days by population origin for location and year. Residuals were well distributed based on residual and predicted value plots. Questions addressed by the analyses were: 1) was there a difference in yield, reproductive tiller production, or germination between two jointed goatgrass populations of similar origin; 2) was this difference consistent across a range of vernalization days; 3) what was the effect of vernalization on yield, reproductive tiller production, and germination; and 4) did this effect vary with population, location, or year. Comparisons within jointed goatgrass populations of similar origin were made with Type 3 Tests of main effects and interactions (α=0.05), while confidence intervals (α=0.05) on predicted intercepts and slopes were used to evaluate the responses among populations within a location and year. When the slopes and intercepts of two fitted lines from paired populations did not differ for a given agronomic characteristic, data were pooled, and analyses were rerun.

To simplify interpretations of the regression line slopes, the algebraic identity

$$m=1(1/m) \qquad [2.1]$$

was used to transform the slope into the context of the number of additional vernalization days required to increase yield, reproductive tiller production, or germination by one unit.

Results and Discussion

Partial or complete fulfillment of the vernalization requirement results in accelerated flowering (Chouard 1960). A shortened vegetative period leads to fewer leaves, spikelets, and tillers on mature plants, and subsequently, vernalized plants have reduced yields compared to unvernalized plants that are allowed to complete their life cycle (Cooper 1956; Levy and Peterson 1972; Wall and Cartwright 1974). Within the constraints of a typical wheat growing season, however, unvernalized plants do not usually yield, and are destroyed by tillage or herbicide application after harvest. Therefore, we reason that an *increased* yield measurement is a justifiable parameter to evaluate as a vernalization response. Additionally, spikelets on mature jointed goatgrass plants often shatter before harvest. Because shattering deflates yield numbers, reproductive tiller numbers were recorded also to provide yield estimates. As with yield, an increase in reproductive tiller production represented a positive vernalization response. The results of germination tests were used as indicators of seed quality. Although two populations or plant types may have similarly produced spikes at harvest, spikes on plants with fulfilled vernalization requirements may have matured earlier, and would contain seed that germinate to greater final percentages compared to partially vernalized plants.

Correlation coefficients on agronomic characteristic measurements in these studies were: yield vs. reproductive tillers r=0.85; yield vs. germination r=0.39; and reproductive tillers vs. germination r=0.24. Models were run separately on yield and reproductive tillers as a function of vernalization days by population origin for each location and year. Low correlation coefficients between yield and germination and reproductive tillers and germination may have resulted because seed failed to develop inside jointed goatgrass spikelets. Correlation coefficients may have been higher for winter and spring wheat.

'Roadside' and 'winter' populations originating from Bickleton, WA, did not differ in yield, reproductive tiller production, or germinability. Neither the slopes nor intercepts between populations for agronomic characteristics as functions of vernalization days were different (data not shown). Bickleton origin plants grown at Corvallis required a minimum of 57 and 78 vernalization days to head in 2003 and 2004, respectively (data not shown). Plants grown at Moro required a minimum of 60 vernalization days in both years. A minimum of 34 and 44 vernalization days were required by plants to head at Pendleton, in 2003 and 2004, respectively. Yield, reproductive tillers, and germination were positively influenced by vernalization days (Fig. 2.1). Yields and reproductive tiller numbers were greatest at Pendleton, and more affected by vernalization than at Moro or Corvallis (Table 2.4). Between seven and nine vernalization days were needed to increase yields 1.0 g at Pendleton, but 11-20 vernalization days were needed to increase yields at Moro, and 25-33 vernalization days were needed to increase yields at Corvallis.

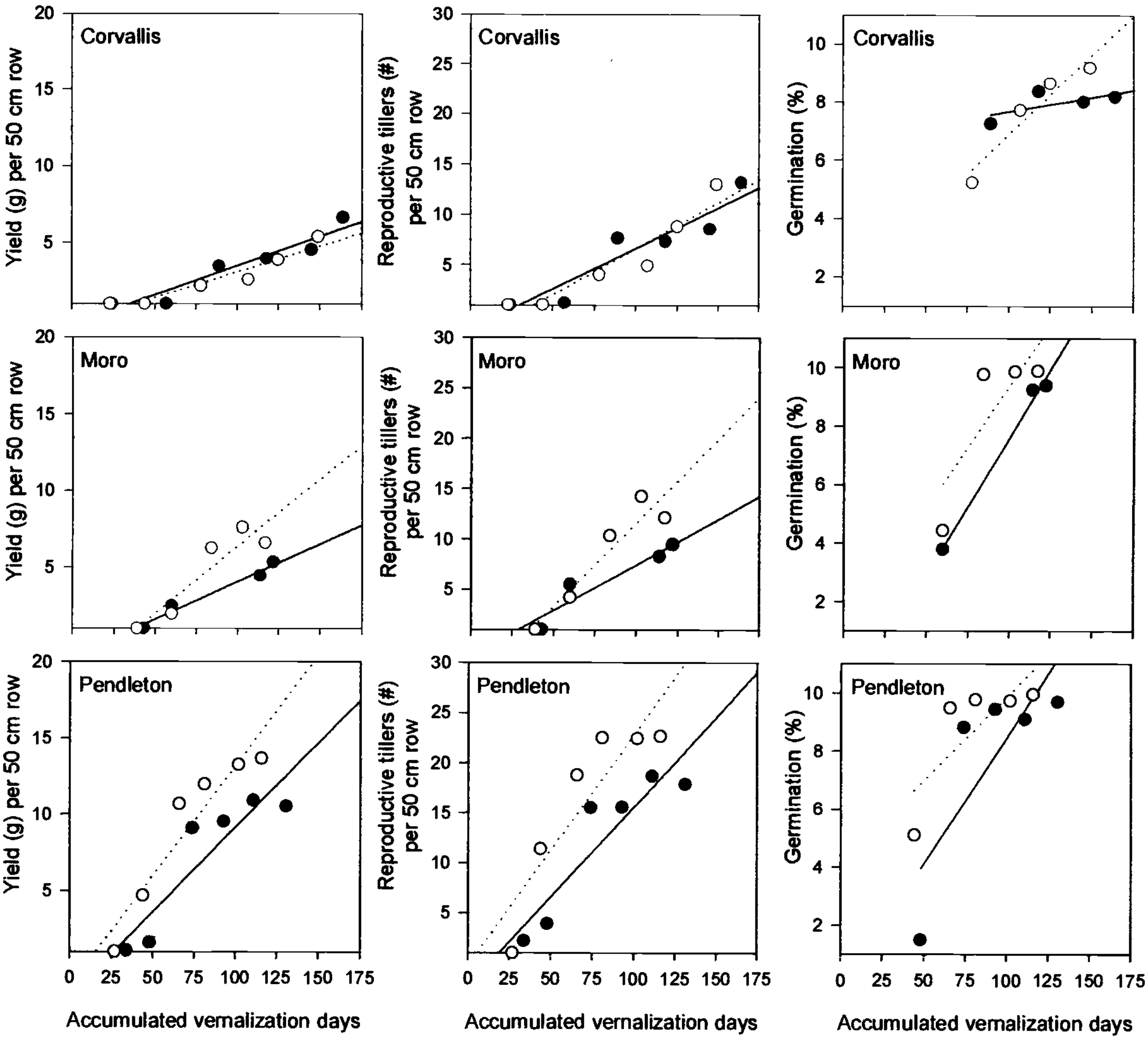

Figure 2.1. Regression of the square root of yield, reproductive tiller production, and germination percentage on accumulated vernalization days for populations originating at Bickleton, WA, and grown over the 2002-2004 seasons at Corvallis, Moro, and Pendleton, OR. Solid circles and lines —●— represent actual and predicted values for various characteristics of plants grown during 2002-03, while open circles and dashed lines --○-- represent actual and predicted values for various characteristics of plants grown during 2003-04. Axes are not the same for all characteristics.

Table 2.4. Linear equations and coefficient confidence intervals (CI) (α=0.05) for the regression of various characteristics on vernalization days (VD) for jointed goatgrass populations originating at Bickleton, WA, and grown over the 2002-2004 seasons at Corvallis, Moro, and Pendleton, OR.

Char.[a]	Loc.[b]	Population[c]	Year[d]	Equation	Lower CI Int.[e]	Upper CI Int.	Lower CI Slope	Upper CI Slope	1/Slope
Yield	Corv.	Bickleton - combined	2002	-0.30+0.04(VD)	-1.02	0.42	0.03	0.04	25
Yield	Corv.	Bickleton - combined	2003	-0.27+0.03(VD)	-0.93	0.39	0.03	0.04	33
Yield	Moro	Bickleton - combined	2002	-0.82+0.05(VD)	-1.92	0.28	0.04	0.06	20
Yield	Moro	Bickleton - combined	2003	-2.36+0.09(VD)	-3.99	-0.72	0.07	0.11	11
Yield	Pend.	Bickleton - combined	2002	-1.93+0.11(VD)	-3.88	0.03	0.09	0.13	9
Yield	Pend.	Bickleton - combined	2003	-1.26+0.14(VD)	-3.11	0.58	0.12	0.17	7
Tillers	Corv.	Bickleton - combined	2002	-1.41+0.08(VD)	-3.19	0.37	0.06	0.10	13
Tillers	Corv.	Bickleton - combined	2003	-2.52+0.09(VD)	-3.99	-1.05	0.08	0.11	11
Tillers	Moro	Bickleton - combined	2002	-1.61+0.09(VD)	-4.35	1.14	0.06	0.12	11
Tillers	Moro	Bickleton - combined	2003	-5.05+0.17(VD)	-7.80	-2.29	0.13	0.20	6
Tillers	Pend.	Bickleton - combined	2002	-2.41+0.18(VD)	-5.68	0.85	0.14	0.22	6
Tillers	Pend.	Bickleton - combined	2003	-0.32+0.23(VD)	-3.93	3.29	0.19	0.28	4
Germ.	Corv.	Bickleton - combined	2002	6.69+0.01(VD)	5.27	8.11	0.00	0.02	100
Germ.	Corv.	Bickleton - combined	2003	1.43+0.05(VD)	-1.03	3.89	0.03	0.07	20
Germ.	Moro	Bickleton - combined	2002	-1.82+0.09(VD)	-3.25	-0.39	0.08	0.11	11
Germ.	Moro	Bickleton - combined	2003	1.02+0.08(VD)	-2.99	5.02	0.04	0.13	13
Germ.	Pend.	Bickleton - combined	2002	-0.22+0.09(VD)	-2.78	2.34	0.06	0.11	11
Germ.	Pend.	Bickleton - combined	2003	4.13+0.06(VD)	2.27	6.00	0.04	0.08	17

[a] Yield measured in g across 50 cm of row; Tillers counted across 50 cm of row; Germination (Germ.) was scored 14 d after incubation at 25/15 C day/night temperatures and a 12-h photoperiod.

[b] Corv.=Corvallis, OR; Pend.=Pendleton, OR.

[c] There were no yield, tiller production, or germination percentage differences between populations.

[d] Year denotes the fall the study was initiated.

[e] Confidence intervals were calculated using α=0.05. Int.=regression line intercept.

'Spring' and 'winter' populations originating from The Dalles, OR, did not differ in yield or reproductive tiller production, but were different in germination. The Dalles origin plants grown at Corvallis required a minimum of 89 and 78 vernalization days to head in 2003 and 2004, respectively (data not shown). Plants grown at Moro required a minimum of 60 vernalization days in both years. A minimum of 48 vernalization days in 2002-03 and 44 vernalization days in 2003-04 were required by plants to head at Pendleton. Plants originating from The Dalles yielded more and produced more reproductive tillers as vernalization days increased (Fig. 2.2). The effects of experiment location on yield and reproductive tiller production on plants originating from The Dalles was similar to the effects observed on Bickleton origin plants. Approximately 10-11 vernalization days were needed to increase yields 1.0 g at Pendleton, 10-17 vernalization days were needed to increase yields at Moro, and 25 vernalization days were needed to increase yields at Corvallis (Table 2.5). Germination was affected by population and vernalization days. Although the 'winter' population produced spikes with 60 vernalization days at Moro in 2002-03 and 2003-04, spikelets were green and seed did not germinate (Fig. 2.2). A minimum of 114 vernalization days in 2002-03 and 84 vernalization days in 2003-04 were required to produce germinable seed of The Dalles 'winter' population at Moro. In contrast, seed from the 'spring' population germinated to 12% in 2002-03 and to 1% in 2003-04 with 60 vernalization days. The 'winter' population required also 22 more vernalization days to produce germinable seed at Pendleton in 2003-04 compared to the 'spring' population. Differential germination patterns were not observed when the populations were grown at Corvallis, or during the 2002-03 season at Pendleton.

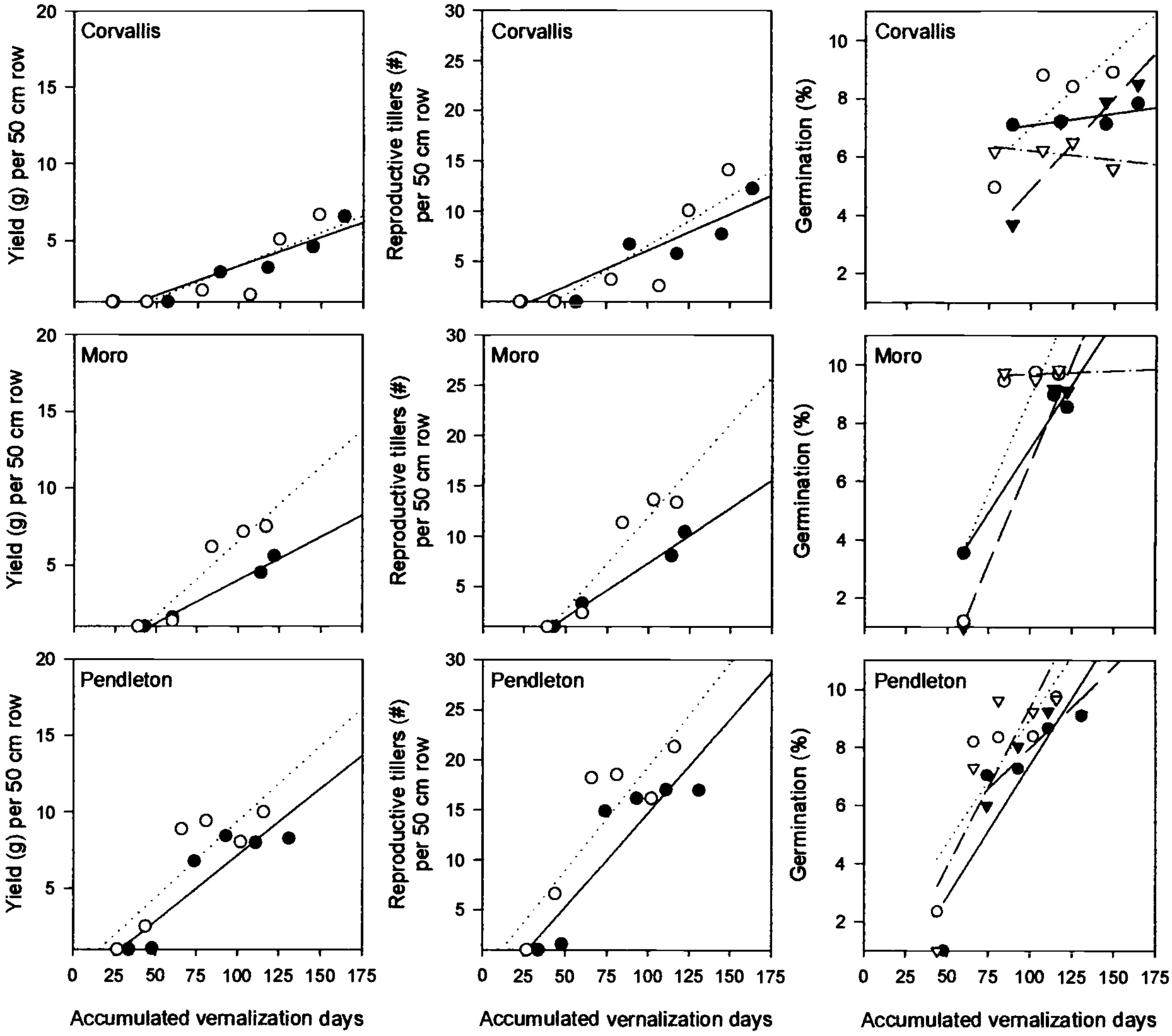

Figure 2.2. Regression of the square root of yield, reproductive tiller production, and germination percentage on accumulated vernalization days for populations originating at The Dalles, OR, and grown over the 2002-2004 seasons at Corvallis, Moro, and Pendleton, OR. Solid circles and lines —●— represent actual and predicted values for various characteristics of 'spring' type jointed goatgrass plants grown during 2002-03, while open circles and dashed lines --O-- represent actual and predicted values for various characteristics of 'spring' type jointed goatgrass plants grown during 2003-04. Solid triangles and dotted lines –▼– represent actual and predicted values for various characteristics of 'winter' type jointed goatgrass plants grown during 2002-03, while open triangles and dash-dot lines –▽– represent actual and predicted values for various characteristics of 'winter' type jointed goatgrass plants grown during 2003-04. Axes are not the same for all characteristics.

Table 2.5. Linear equations and coefficient confidence intervals (CI) ($\alpha=0.05$) for the regression of various characteristics on vernalization days (VD) for jointed goatgrass populations originating at The Dalles, OR, and grown over the 2002-2004 seasons at Corvallis, Moro, and Pendleton, OR.

Char.[a]	Loc.[b]	Population[c]	Year[d]	Equation	Lower CI Int.[e]	Upper CI Int.	Lower CI Slope	Upper CI Slope	1/Slope
Yield	Corv.	The Dalles - combined	2002	-0.45+0.04(VD)	-1.34	0.44	0.03	0.05	25
Yield	Corv.	The Dalles - combined	2003	-0.95+0.04(VD)	-1.91	0.01	0.03	0.05	25
Yield	Moro	The Dalles - combined	2002	-1.60+0.06(VD)	-2.36	-0.84	0.05	0.06	17
Yield	Moro	The Dalles - combined	2003	-3.15+0.10(VD)	-4.72	-1.58	0.08	0.12	10
Yield	Pend.	The Dalles - combined	2002	-1.51+0.09(VD)	-3.05	0.04	0.07	0.10	11
Yield	Pend.	The Dalles - combined	2003	-0.56+0.10(VD)	-2.50	1.38	0.07	0.12	10
Tillers	Corv.	The Dalles - combined	2002	-1.16+0.07(VD)	-3.09	0.77	0.06	0.09	14
Tillers	Corv.	The Dalles - combined	2003	-3.30+0.10(VD)	-5.29	-1.32	0.08	0.12	10
Tillers	Moro	The Dalles - combined	2002	-3.54+0.11(VD)	-5.47	-1.60	0.09	0.13	9
Tillers	Moro	The Dalles - combined	2003	-6.59+0.19(VD)	-9.23	-3.95	0.15	0.22	5
Tillers	Pend.	The Dalles - combined	2002	-4.12+0.19(VD)	-7.41	-0.83	0.15	0.23	5
Tillers	Pend.	The Dalles - combined	2003	-1.45+0.21(VD)	-5.14	2.24	0.16	0.25	5

[a] Yield measured in g across 50 cm of row; Tillers counted across 50 cm of row; Germination (Germ.) was scored 14 d after incubation at 25/15 C day/night temperatures and a 12-h photoperiod.

[b] Corv.=Corvallis, OR; Pend.=Pendleton, OR.

[c] There were no yield or tiller production differences between populations and data were combined. Germination data were analyzed by population.

[d] Year denotes the fall the study was initiated.

[e] Confidence intervals were calculated using $\alpha=0.05$. Int.=regression line intercept.

Table 2.5 (Continued). Linear equations and coefficient confidence intervals (CI) (α=0.05) for the regression of various characteristics on vernalization days (VD) for jointed goatgrass populations originating at The Dalles, OR, and grown over the 2002-2004 seasons at Corvallis, Moro, and Pendleton, OR.

Char.[a]	Loc.[b]	Population[c]	Year[d]	Equation	Lower CI Int.[e]	Upper CI Int.	Lower CI Slope	Upper CI Slope	1/Slope
Germ.	Corv.	The Dalles - S	2002	6.28+0.00(VD)	3.34	9.24	-0.01	0.03	n/a
Germ.	Corv.	The Dalles - W	2002	-1.38+0.06(VD)	-4.39	1.62	0.04	0.09	17
Germ.	Corv.	The Dalles - S	2003	1.75+0.05(VD)	-3.25	6.77	0.01	0.09	20
Germ.	Corv.	The Dalles - W	2003	6.82-0.00(VD)	1.69	11.97	-0.05	0.04	n/a
Germ.	Moro	The Dalles - S	2002	-1.63+0.08(VD)	-3.53	0.25	0.07	0.11	13
Germ.	Moro	The Dalles - W	2002	-7.12+0.13(VD)	-9.39	-4.86	0.12	0.16	8
Germ.	Moro	The Dalles - S	2003	-4.20+0.13(VD)	-9.08	0.67	0.08	0.18	8
Germ.	Moro	The Dalles - W	2003	9.46+0.00(VD)	0.92	18.00	-0.08	0.09	n/a
Germ.	Pend.	The Dalles - S	2002	-1.68+0.09(VD)	-3.92	0.56	0.07	0.11	11
Germ.	Pend.	The Dalles - W	2002	2.38+0.05(VD)	-1.33	6.10	0.02	0.09	20
Germ.	Pend.	The Dalles - S	2003	0.42+0.08(VD)	-2.83	3.68	0.05	0.12	13
Germ.	Pend.	The Dalles - W	2003	-1.58+0.10(VD)	-4.84	1.68	0.07	0.15	10

[a] Yield measured in g across 50 cm of row; Tillers counted across 50 cm of row; Germination (Germ.) was scored 14 d after incubation at 25/15 C day/night temperatures and a 12-h photoperiod.

[b] Corv.=Corvallis, OR; Pend.=Pendleton, OR.

[c] There were no yield or tiller production differences between populations and data were combined. Germination data were analyzed by population.

[d] Year denotes the fall the study was initiated.

[e] Confidence intervals were calculated using α=0.05. Int.=regression line intercept.

‘Spring’ and ‘winter’ populations originating from Helix, OR, did not differ in yield, tiller production, or germinability. The slopes and intercepts between population and vernalization days for all agronomic characteristics were not different (data not shown). Helix origin plants at Corvallis required a minimum of 57 and 78 vernalization days to head in 2002-03 and 2003-04, respectively (data not shown). Plants at Moro required a minimum of 60 vernalization days in both years. A minimum of 48 and 44 vernalization days were required by Helix origin plants to head at Pendleton in 2002-03 and 2003-04, respectively. Yield, reproductive tillers, and germination percentages were positively influenced by vernalization days (Fig. 2.3), and were greatest at Pendleton, OR. Increasing vernalization days increased yields of Helix origin plants at rates similar to those reported for Bickleton and The Dalles origin plants (Table 2.6).

Spring wheat agronomic characteristics plotted against vernalization days did not show positive, linear relationships (Fig. 2.4). Yield and tiller distributions were bimodal; plants produced reproductive tillers and spikes during fall plantings (Oct and Nov), plants did not survive winter sowings (Dec and Jan), and plants were successful when sown in the spring. Regression models indicated that yield and reproductive tiller production were not influenced by vernalization days (Table 2.7), and slope confidence intervals centered on zero. Germinability also was not affected by vernalization days. Plants sown on all planting dates produced seed that germinated from 98-100% (Fig. 2.4). Spring wheat yield and reproductive tiller production were influenced by vernalization days at Corvallis in both years. Mild winters at Corvallis compared to Pendleton and Moro may have contributed to the success of fall and winter sown spring wheat plants at that site.

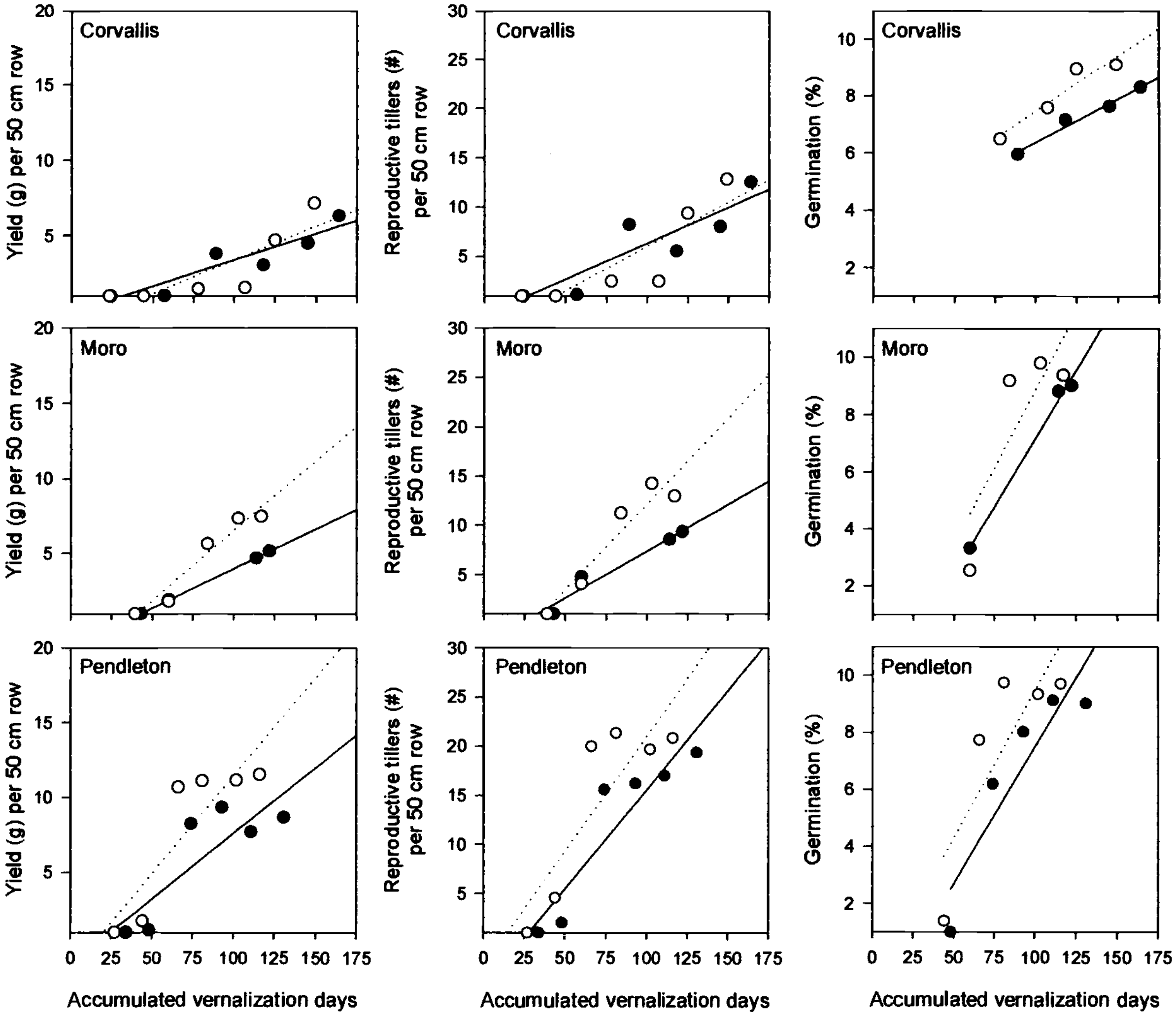

Figure 2.3. Regression of the square root of yield, reproductive tiller production, and germination percentage on accumulated vernalization days for populations originating at Helix, OR, and grown over the 2002-2004 seasons at Corvallis, Moro, and Pendleton, OR. Solid circles and lines —●— represent actual and predicted values for various characteristics of plants grown during 2002-03, while open circles and dashed lines --○-- represent actual and predicted values for various characteristics of plants grown during 2003-04. Axes are not the same for all characteristics.

Table 2.6. Linear equations and coefficient confidence intervals (CI) (α=0.05) for the regression of various characteristics on vernalization days (VD) for jointed goatgrass populations originating at Helix, OR, and grown over the 2002-2004 seasons at Corvallis, Moro, and Pendleton, OR.

Char.[a]	Loc.[b]	Population[c]	Year[d]	Equation	Lower CI Int.[e]	Upper CI Int.	Lower CI Slope	Upper CI Slope	1/Slope
Yield	Corv.	Helix - combined	2002	-0.07+0.03(VD)	-0.87	0.73	0.03	0.04	33
Yield	Corv.	Helix - combined	2003	-1.04+0.04(VD)	-2.06	-0.03	0.03	0.05	25
Yield	Moro	Helix - combined	2002	-1.23+0.05(VD)	-2.06	-0.41	0.04	0.06	20
Yield	Moro	Helix - combined	2003	-2.74+0.09(VD)	-3.98	-1.51	0.08	0.11	11
Yield	Pend.	Helix - combined	2002	-1.14+0.09(VD)	-3.11	0.83	0.07	0.11	11
Yield	Pend.	Helix - combined	2003	-1.61+0.13(VD)	-3.73	0.50	0.10	0.16	8
Tillers	Corv.	Helix - combined	2002	-0.90+0.07(VD)	-2.87	1.06	0.06	0.09	14
Tillers	Corv.	Helix - combined	2003	-2.94+0.09(VD)	-4.83	-1.05	0.07	0.11	11
Tillers	Moro	Helix - combined	2002	-2.14+0.09(VD)	-4.07	-0.21	0.07	0.12	11
Tillers	Moro	Helix - combined	2003	-5.28+0.17(VD)	-8.03	-2.54	0.14	0.21	6
Tillers	Pend.	Helix - combined	2002	-4.64+0.20(VD)	-7.84	-1.44	0.17	0.24	5
Tillers	Pend.	Helix - combined	2003	-2.45+0.23(VD)	-6.65	1.75	0.18	0.29	4
Germ.	Corv.	Helix - combined	2002	3.36+0.03(VD)	1.93	4.78	0.02	0.04	33
Germ.	Corv.	Helix - combined	2003	3.58+0.04(VD)	1.27	5.88	0.02	0.06	25
Germ.	Moro	Helix - combined	2002	-2.38+0.10(VD)	-3.27	-1.48	0.09	0.10	10
Germ.	Moro	Helix - combined	2003	-1.95+0.11(VD)	-5.58	1.69	0.07	0.15	9
Germ.	Pend.	Helix - combined	2002	-2.11+0.10(VD)	-3.87	-0.35	0.08	0.11	10
Germ.	Pend.	Helix - combined	2003	-0.92+0.10(VD)	-3.34	1.50	0.08	0.13	10

[a] Yield measured in g across 50 cm of row; Tillers counted across 50 cm of row; Germination (Germ.) was scored 14 d after incubation at 25/15 C day/night temperatures and 12-h photoperiod.

[b] Corv.=Corvallis, OR; Pend.=Pendleton, OR.

[c] There were no yield, tiller production, or germination percentage differences between populations and data were combined.

[d] Year denotes the fall the study was initiated.

[e] Confidence intervals were calculated using α=0.05. Int.=regression line intercept.

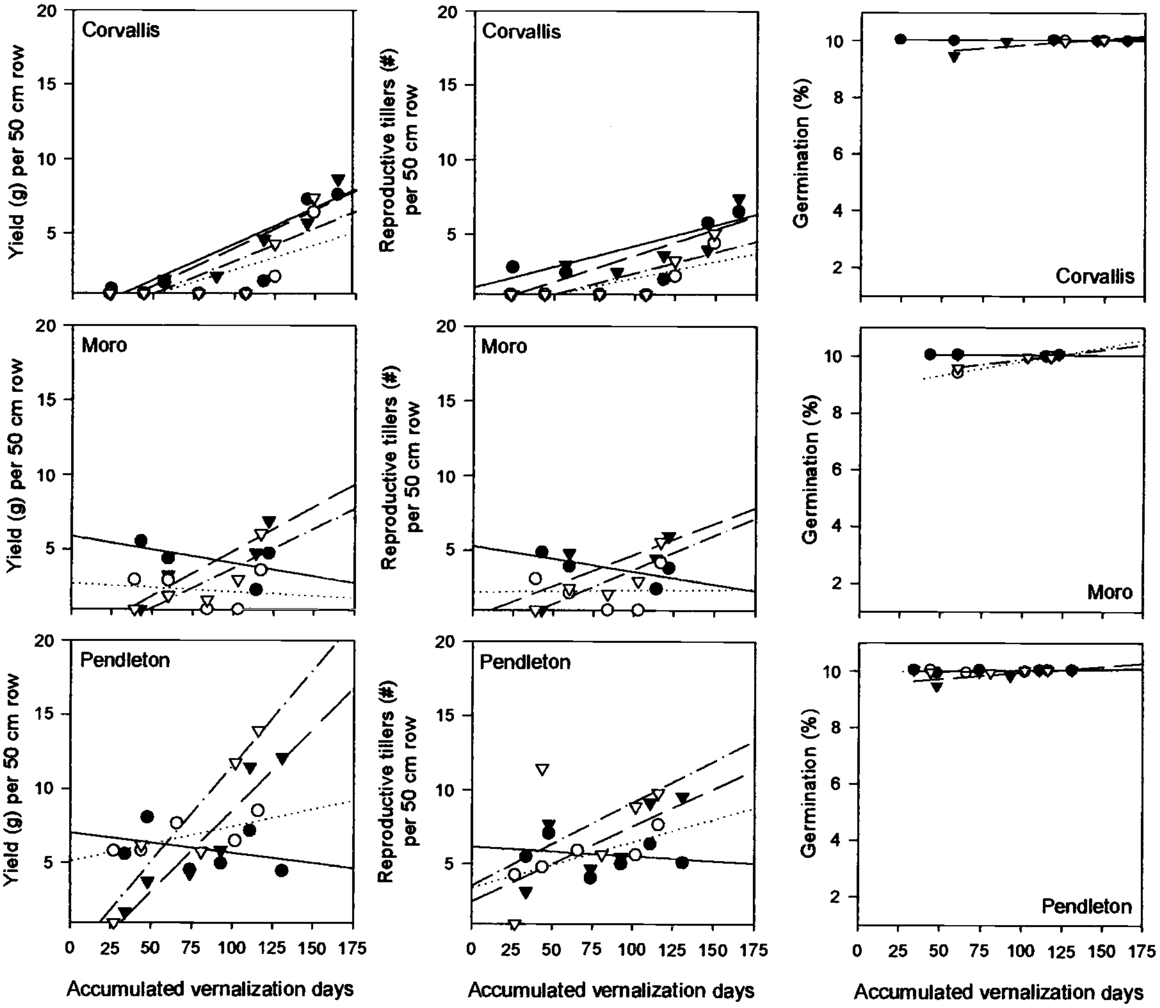

Figure 2.4. Regression of the square root of yield, reproductive tiller production, and germination percentage on accumulated vernalization days for winter and spring wheat grown over the 2002-2004 seasons at Corvallis, Moro, and Pendleton, OR. Solid circles and lines —●— represent actual and predicted values for various characteristics of spring wheat grown during 2002-03, while open circles and dashed lines --○-- represent actual and predicted values for various characteristics of spring wheat grown during 2003-04. Solid triangles and dotted lines –▼– represent actual and predicted values for various characteristics of winter wheat grown during 2002-03, while open triangles and dash-dot lines –·▽·– represent actual and predicted values for various characteristics of winter wheat grown during 2003-04. Axes are not the same for all characteristics.

Table 2.7. Linear equations and coefficient confidence intervals (CI) (α=0.05) for the regression of various characteristics on vernalization days (VD) for winter wheat and spring wheat grown over the 2002-2004 seasons at Corvallis, Moro, and Pendleton, OR.

Char.[a]	Loc.[b]	Population[c]	Year[d]	Equation	Lower CI Int.[e]	Upper CI Int.	Lower CI Slope	Upper CI Slope	1/Slope
Yield	Corv.	SW	2002	-0.51+0.04(VD)	-2.01	0.99	0.04	0.06	25
Yield	Corv.	SW	2003	-0.75+0.03(VD)	-2.44	0.93	0.02	0.05	33
Yield	Moro	SW	2002	5.87-0.01(VD)	4.03	7.72	-0.04	0.00	100
Yield	Moro	SW	2003	2.71-0.00(VD)	0.29	5.15	-0.03	0.02	n/a
Yield	Pend.	SW	2002	7.02-0.01(VD)	5.07	8.99	-0.04	0.01	100
Yield	Pend.	SW	2003	5.11+0.02(VD)	2.58	7.65	-0.01	0.05	50
Yield	Corv.	WW	2002	-1.05+0.05(VD)	-2.49	0.38	0.04	0.06	20
Yield	Corv.	WW	2003	-1.23+0.04(VD)	-2.92	0.44	0.03	0.06	25
Yield	Moro	WW	2002	-1.04+0.05(VD)	-2.88	0.78	0.04	0.08	20
Yield	Moro	WW	2003	-1.53+0.05(VD)	-3.88	0.81	0.03	0.08	20
Yield	Pend.	WW	2002	-2.42+0.10(VD)	-4.37	-0.49	0.09	0.13	10
Yield	Pend.	WW	2003	-1.40+0.12(VD)	-3.68	0.88	0.10	0.16	8
Tillers	Corv.	SW	2002	1.43+0.02(VD)	0.05	2.81	0.02	0.04	50
Tillers	Corv.	SW	2003	-0.15+0.02(VD)	-1.21	0.89	0.01	0.03	50
Tillers	Moro	SW	2002	5.28-0.01(VD)	3.25	7.31	-0.04	0.01	100
Tillers	Moro	SW	2003	2.71+0.00(VD)	-0.06	4.41	-0.02	0.03	n/a
Tillers	Pend.	SW	2002	6.14-0.00(VD)	3.73	8.57	-0.03	0.02	n/a
Tillers	Pend.	SW	2003	3.39+0.03(VD)	-0.71	7.50	-0.02	0.08	33
Tillers	Corv.	WW	2002	0.08+0.03(VD)	-1.24	1.40	0.02	0.05	33
Tillers	Corv.	WW	2003	-0.44+0.02(VD)	-1.49	0.61	0.02	0.04	50
Tillers	Moro	WW	2002	0.50+0.04(VD)	-1.50	2.52	0.02	0.06	25
Tillers	Moro	WW	2003	-0.90+0.04(VD)	-3.05	1.25	0.02	0.07	25
Tillers	Pend.	WW	2002	2.46+0.05(VD)	0.07	4.86	0.02	0.08	20
Tillers	Pend.	WW	2003	3.53+0.05(VD)	-0.16	7.23	0.01	0.10	20

[a] Yield measured in g across 50 cm of row; Tillers counted across 50 cm of row; Germination (Germ.) was scored 14 d after incubation at 25/15 C day/night temperatures and 12-h photoperiod.

[b] Corv.=Corvallis, OR; Pend.=Pendleton, OR.

[c] SW=spring wheat; WW=winter wheat. There were yield, tiller production, and germination percentage differences between winter and spring wheat.

[d] Year denotes the fall the study was initiated.

[e] Confidence intervals were calculated using α=0.05. Int.=regression line intercept.

Table 2.7 (Continued). Linear equations and coefficient confidence intervals (CI) (α=0.05) for the regression of various characteristics on vernalization days (VD) for winter wheat and spring wheat grown over the 2002-2004 seasons at Corvallis, Moro, and Pendleton, OR.

Char.[a]	Loc.[b]	Population[c]	Year[d]	Equation	Lower CI Int.[e]	Upper CI Int.	Lower CI Slope	Upper CI Slope	1/Slope
Germ.	Corv.	SW	2002	10.04-0.00(VD)	9.87	10.22	0.00	0.00	n/a
Germ.	Corv.	SW	2003	10.03+0.00(VD)	9.65	10.41	0.00	0.00	n/a
Germ.	Moro	SW	2002	10.06-0.00(VD)	10.01	10.12	0.00	0.00	n/a
Germ.	Moro	SW	2003	8.80+0.01(VD)	8.29	9.31	0.01	0.01	100
Germ.	Pend.	SW	2002	9.98+0.00(VD)	9.55	10.42	0.00	0.01	n/a
Germ.	Pend.	SW	2003	9.98+0.00(VD)	9.82	10.14	0.00	0.00	n/a
Germ.	Corv.	WW	2002	9.39+0.00(VD)	9.14	9.66	0.00	0.01	n/a
Germ.	Corv.	WW	2003	9.67+0.00(VD)	9.34	10.01	0.00	0.00	n/a
Germ.	Moro	WW	2002	10.06-0.00(VD)	9.98	10.15	0.00	0.00	n/a
Germ.	Moro	WW	2003	9.17+0.00(VD)	8.80	9.55	0.00	0.01	n/a
Germ.	Pend.	WW	2002	9.49+0.00(VD)	8.98	10.02	0.00	0.01	n/a
Germ.	Pend.	WW	2003	9.92+0.00(VD)	9.82	10.03	0.00	0.00	n/a

[a] Yield measured in g across 50 cm of row; Tillers counted across 50 cm of row; Germination (Germ.) was scored 14 d after incubation at 25/15 C day/night temperatures and 12-h photoperiod.

[b] Corv.=Corvallis, OR; Pend.=Pendleton, OR.

[c] SW=spring wheat; WW=winter wheat. There were yield, tiller production, and germination percentage differences between winter and spring wheat.

[d] Year denotes the fall the study was initiated.

[e] Confidence intervals were calculated using α=0.05. Int.=regression line intercept.

Winter wheat agronomic characteristics regressed against vernalization days revealed positive linear relationships similar to jointed goatgrass. Wheat plants at Corvallis required a minimum of 57 and 125 vernalization days to head in 2002-03 and 2003-04, respectively (data not shown). Plants at Moro required a minimum of 60 vernalization days in both years. A minimum of 34 and 44 vernalization days were required by winter wheat plants to head at Pendleton in 2002-03 and 2003-04, respectively. Yield and reproductive tillers were positively influenced by vernalization days (Fig. 2.4). Approximately eight to ten vernalization days were needed to increase yields 1.0 g at Pendleton, and 20-25 vernalization days were needed to increase yields at Moro and Corvallis (Table 2.7). Germination was not affected by vernalization. Germination of winter wheat seed across all planting dates ranged from 89-100% (Fig. 4).

Jointed goatgrass vernalization requirements varied with location and year when compared to winter wheat. In 2002-03, winter wheat consistently yielded more, produced more reproductive tillers, and produced seed that was more germinable than jointed goatgrass on the last successful planting date for both species at all sites (Feb 24 at Corvallis, Mar 3 at Moro, and Mar 24 at Pendleton). Similar trends were observed at Moro and Pendleton in 2003-04. However, the pattern was not consistent at Corvallis in 2003-04. Jointed goatgrass planted on Dec 15 (107 VD) and Jan 22 (78 VD) reproduced, whereas winter wheat was unsuccessful. A factor other than vernalization temperatures, such as available moisture, may have contributed to the reproductive success of jointed goatgrass at Corvallis in 2003-04. Spring wheat planted in the spring at Corvallis in 2003-04 also did not reproduce. In general, jointed goatgrass required a greater number of vernalization days to reproduce compared to winter wheat. Once the requirement was met, jointed goatgrass and wheat yields responded similarly to increasing vernalization days (Tables 2.4-2.7, slope parameter). However, jointed goatgrass produced reproductive tillers at twice the rate of wheat as vernalization days increased. Germination of jointed goatgrass seed was also more affected by vernalization than wheat seed.

Jointed goatgrass vernalization requirements varied among populations within a location and year. Plants from populations that originated at The Dalles remained vegetative when exposed to 57 vernalization days (Feb 24 planting) at Corvallis in 2002-03, while Bickleton and Helix origin plants reproduced. These differences were not observed in 2003-04, probably because the next earliest planting date for any population to head resulted in 78 VD exposure. Additionally, 'winter' type plants of The Dalles origin planted on Mar 3, 2003 did not produce germinable seed, but plants of the 'spring' type produced seed that germinated to 12% (see above). Populations originating from Bickleton were usually the first to begin heading (personal observation). Amplitude in vernalization requirements and development responses likely contributes to the adaptability of jointed goatgrass in variable habitats across as the western United States. Although the jointed goatgrass populations used in these studies were different in their responses to vernalization, a true 'spring' type or vernalization insensitive population was not identified. However, if spring time temperatures were cool, jointed goatgrass plants could produce germinable seed with as little as 44 vernalization days, thus reducing the benefits of planting spring crops.

Genetically distinct spring and winter types of wild tetraploid wheat were identified in Israel (Kushnir and Halloran 1982). The authors reported that vernalization type was related to the elevation of the collection site. Spring types were found at sea level, where the photoperiod and temperatures were more constant over the growing season. Winter types were found 1400 m above sea level on a mountain slope, where the photoperiod and temperature changes were more dramatic. Efforts to evaluate jointed goatgrass population polymorphism could be improved with collections from environments more diverse than those reported in the current study, or by selection of populations reported as most genetically distinct (Hegde et al. 2002; Pester et al. 2003).

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Sources of Materials

[1] Osmocote 14-14-14. The Scotts Company, 14111 Scottslawn Road, Marysville, OH 43041.

[2] BB44 Steel Blue Blotter. Hoffman Manufacturing Inc., International Agri-Supply, 353 29th Avenue SW, Albany, OR 97321.

[3] Cont156C Transparent Acrylic Container. Hoffman Manufacturing Inc., International Agri-Supply, 353 29th Avenue SW, Albany, OR 97321.

[4] SAS, Version 8.2. SAS Institute Inc., Cary, NC, USA.

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CHAPTER 3

Vernalization Requirements of Wheat (*Triticum aestivum* L.) and Wheat by Jointed Goatgrass (*Aegilops cylindrica* Host) Hybrid Plants

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Abbreviations: Cent, Centennial; CI, confidence interval; GDD, growing degree days; Jgg, jointed goatgrass; Mad, Madsen; Temp, temperature; VD, vernalization days.

Recently, selective control of jointed goatgrass in winter wheat became possible through the release of herbicide-resistant wheat cultivars. To assess the risk of gene movement from herbicide-resistant winter wheat to jointed goatgrass, information about the reproductive development of wheat and wheat by jointed goatgrass hybrid plants is required. Madsen, Centennial, and reciprocal hybrid seedlings were exposed from 0 to 8-wk vernalization at 4, 7, and 10 C. Tiller production and growth stages were recorded for plants grown over 13 weeks in the greenhouse. All unvernalized and vernalized Centennial and Centennial related plants reached the joint stage (one reproductive node) by the end of the experiment. The minimum vernalization treatment for any Madsen plant to joint by the end of the experiment was 2-wk at 4 C, for any Madsen by jointed goatgrass plant was 2-wk at 7 C, and for any jointed goatgrass by Madsen plant was 4-wk at 4 C. Reciprocal crosses between spring wheat and jointed goatgrass produced hybrid plants that were nearly insensitive to vernalization. Synchronous reproductive development between Madsen and Madsen by jointed goatgrass plants in response to varying vernalization conditions increases the risks for the transfer of wheat genes into jointed goatgrass populations. To reduce the risk of gene flow, hybrid plants should be identified via field scouting and removed, and only certified wheat seed should be planted in jointed goatgrass infested fields.

Jointed goatgrass ($2n = 4x = 28$; CCDD) infestations in winter wheat ($2n = 6x = 42$; AABBDD) production regions of the central and western USA result in $145 million annual losses in the wheat market (Anonymous 2004). Because jointed goatgrass and wheat are genetically related, and their life histories are similar (Ball et al., 1995; Miller 1995; Dotray and Young 1988; Fenster and Wicks 1976; Johnston and Parker 1929), strategies for jointed goatgrass control have been limited to cultural practices, crop rotation, and tillage. Recently, selective control of jointed goatgrass in winter wheat became possible through the release of herbicide-resistant wheat cultivars (Haley et al., 2003; Lazar et al., 2003). However, the possible transfer of a herbicide-resistance gene from winter wheat to jointed goatgrass poses a threat to the success of this weed-management program. One of the greatest risks involved with the development and release of genetically modified crops is the sexual transfer of genes from a modified crop to its wild relative (Goodman and Newell 1985).

A herbicide-resistance gene might introgress into a jointed goatgrass population due to the sexual compatibility between wheat and jointed goatgrass (Seefeldt et al., 1998; Snyder et al., 2000; Zemetra et al., 1998). The potential for recombination and gene exchange between wheat and jointed goatgrass exists because of homologous D genome chromosome pairing (Kimber and Zhou 1983; Riley and Law 1965; Zemetra et al., 1998). The transfer of a herbicide-resistance gene into jointed goatgrass via a hybrid bridge, followed by backcrossing and restoration of self-fertility, leads to the persistence of a herbicide-resistance gene in a jointed goatgrass population. Occurrences of hybrids with the capacity to produce backcross seed were common in jointed goatgrass infested wheat fields in Oregon (Morrison et al., 2002b) and Oklahoma (Stone and Peeper 2004). Furthermore, fertility of subsequent jointed goatgrass backcross generations increased such that restored, partial self-fertility was present in a BC_2 generation (Wang et al., 2001).

Breaking the gene flow process at the hybrid bridge is one management approach to prevent gene movement from winter wheat to jointed goatgrass. To assess the risk of gene movement from herbicide-resistant winter wheat to jointed goatgrass, information about the phenology and reproductive development of winter wheat and wheat by jointed goatgrass hybrid plants is required. Numerous studies have documented the variability in developmental responses of cultivated wheat to vernalization, but the context of its vernalization requirement compared to wheat by jointed goatgrass hybrid plants remains unknown. Synchronous development between winter wheat and hybrid plants at the anthesis stage after exposure to varied vernalization conditions would increase the potential for herbicide-resistance gene migration and persistence in jointed goatgrass populations. Hybrid infestations have been observed also in Oregon spring wheat and spring barley fields during surveys conducted from 1998-2000 (Morrison et al., 2002a), in 2001 (personal observation), and by other researchers (Walenta et al., 2002). Migration of the dominant *Vrn-1* vernalization insensitive allele (Brule-Babel and Fowler 1988) from spring wheat to jointed goatgrass might lead to the development of spring type jointed goatgrass populations, rendering a spring cropping regime ineffective for jointed goatgrass control.

The objective of this research was to quantify the phenology and reproductive development of winter wheat, spring wheat, and wheat by jointed goatgrass reciprocal hybrid plants in response to varying vernalization conditions.

MATERIALS AND METHODS

Wheat by jointed goatgrass and reciprocal hybrid plants were produced in the greenhouse at the University of Idaho using the soft white winter wheat cultivar 'Madsen' (Allan et al., 1989), the soft white spring wheat cultivar 'Centennial' (Souza et al., 1991), and a local population of jointed goatgrass. Plants were emasculated and pollinated by either wheat or jointed goatgrass to produce hybrid seed. All crosses were made by the approach method (Frey 1988). Plants were grown under optimum conditions in the greenhouse. Hybrid spikes were harvested at maturity, seed production recorded, and spikes sent to Oregon State University.

Because determination of vernalization responses under optimum growing conditions in the greenhouse can be time and resource consuming, a low resource procedure developed by Baloch et al., (2003) was modified for use in these studies. Certified Madsen and Centennial seed and seed from each hybrid plant type were placed on two 10.2 by 10.2 cm germination blotters (BB44, Albany, OR) wetted with 25 ml deionized water in similarly sized, clear, covered acrylic germination boxes (Cont156C, Albany, OR). Seed were incubated at 25/15 C day/night temperatures in the dark for 2 d. Six germinated seed from each plant type with consistent radicle lengths were sown 2 cm deep into 3.8-cm diam. by 14-cm depth cones (RLC7 Stubby Cell, Corvallis, OR) filled with potting soil (Sunshine Mix #1/LC 1, Bellevue, WA). Each replication consisted of one germinated seed per cone, and cones were randomly placed into their assigned growth chambers. Growth chambers were set to constant 4, 7, and 10 C temperatures, and lights were set to an 8-h photoperiod (PPFD was not measured). Seedlings were exposed to 0, 2, 4, 5, 6, 6.5, 7, and 8-wk vernalization. All treatment durations were timed so that plants terminated the vernalization period on the same calendar date. After the vernalization treatment, but before transferring to the greenhouse, the temperatures in all growth chambers were set to 10 C for 2 d, raised to 12 C for an additional 2 d, and raised to 15 C for 3 d. Plants were moved into a greenhouse set to 30/18 C day/night temperatures and 16-h photoperiod. Plants were rearranged weekly in both environments to minimize positional effects due to neighboring fans and lights. Plants were watered when the soil surface appeared dry. A commercial water-soluble fertilizer (Peters Professional 20-20-20, Marysville, OH) was prepared according to label directions and applied weekly during both phases of the studies. Plants in the greenhouse were evaluated weekly for pests, and sprayed with nicotine (Fulex Nicotine Fumigator, Woburn, MA) at labeled rates as needed.

The number of tillers produced by each plant was recorded weekly for plants exposed to 0, 4, and 8-wk vernalization. Growth stages on all plants were recorded twice a week. Days from the end of the vernalization period to jointing stage, awn emergence from the boot, full spike emergence from the boot, and the first day of anthesis were recorded. Final evaluations were conducted on Centennial and Centennial related plants approximately seven weeks after the end of the vernalization period, because all plants successfully reached anthesis by this time. All Madsen and Madsen related plants were scored as headed or not headed approximately 13 weeks after the end of the vernalization period. The final number of tillers and the number of tillers with spikes were counted. Spikes were clipped from the culms and stored at 22 ± 2 C in the dark for use in germination studies. Wheat seed were threshed using a stationary thresher. Approximately three weeks after harvest, germination assays were conducted on wheat seed incubated at 25/15 C day/night temperatures and 12-h photoperiod over 14 d. Germination was defined as the presence of 5 mm radicle. Because the hybrids were male sterile and produced no seed, germination assays on hybrids were not conducted. The experiment was repeated.

Greenhouse minimum and maximum daily temperatures were recorded. Growing degree days (GDD) were calculated based on a base temperature of 0 C subtracted from the daily average air temperature (C). Accumulated GDDs were calculated as the sum of daily heat values beginning with the acclimation period in the growth chamber and ending with harvest in the greenhouse. Vernalization days (VD) were calculated as the product of the vernalization temperature and the number of exposed days by treatment (Table 3.1). Two vernalization temperature by duration treatments resulted in the same net accumulated vernalization days – 2-wk at 10 C was identical to 5-wk at 4 C, and 4-wk at 7 C was identical to 7-wk at 4 C.

Table 3.1. Accumulated vernalization days (VD) by vernalization duration and temperature.

		Temperature		
Duration		4 C	7 C	10 C
Wk	D	-----------	VD	-----------
0	0	n/a	n/a	n/a
2	14	56	98	140
4	28	112	196	280
5	35	140	245	350
6	42	168	294	420
6.5	45.5	182	318.5	455
7	49	196	343	490
8	56	224	392	560

Preliminary analysis of the GDD required from acclimation to the joint stage plotted against VD showed negative, linear relationships, and suggested that differences between vernalization durations and temperatures existed for winter wheat, spring wheat, and both hybrid plant types. The minimum vernalization requirement for each wheat cultivar and hybrid plant type to reach jointing and anthesis were estimated from frequency tables. The frequency of plants to reach anthesis was adjusted by the frequency of plants to reach the joint stage. Linear regression using PROC MIXED in SAS (Version 8.2, Cary, NC) for a full factorial design was used to test the main and interaction effects of vernalization duration and temperature by plant type on GDD to the joint stage. Vernalization responses were estimated from the regression functions, and confidence intervals (α=0.05) on model intercepts and slopes were used to compare differences among plants types. Actual values and confidence intervals for GDD to joint by temperature at 8-wk vernalization were used to estimate the point of maximum vernalization for all plant types. Total tiller number per plant for plants vernalized 0, 4, and 8-wk was linearly regressed against GDD. Percentages for reproductive tillers produced per plant and seed germination were calculated. The minimum vernalization requirement for production of reproductive tillers and germination values greater than the responses of unvernalized plants were obtained from PDIFF (α=0.05) tables in SAS.

RESULTS AND DISCUSSION

Environmental conditions in the greenhouse were similar between repeated experiments. Daily minimum and maximum temperatures and accumulated GDD in the greenhouse during the two experiments are shown in Fig. 3.1. Plants were exposed to an average of 22 ± 2.2 GDD per d during run one, and 22 ± 2.3 GDD per d during run two. Because plants within a run were not harvested on the same day, plants in the greenhouse were exposed to 2248-2316 GDD by harvest in run one and to 2214-2275 GDD by harvest in run two. In comparison, the 30-yr average for GDD accumulated during a growing season at Pendleton, OR, an area where winter wheat is a common crop and jointed goatgrass infestations are frequent, was 3084 (data not shown). An alternative calculation for the net GDD accumulated by plants in these studies during exposure to growth chamber and greenhouse temperatures ranged from 2214 (unvernalized) to 2876 (8-wk vernalization at 10 C) GDD. Final GDD values accumulated by plants in these studies approximated the 30-yr average field GDD value.

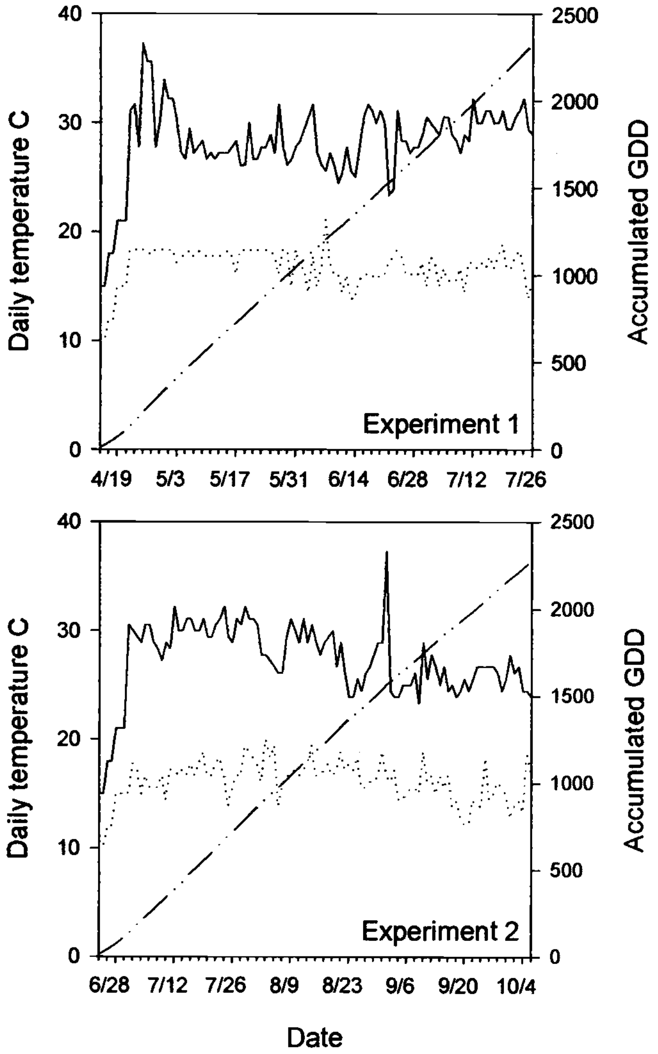

Figure 3.1. Daily minimum and maximum air temperatures recorded in the greenhouse and accumulated growing degree days (GDD) for the two experiments. Solid lines ——— represent daily maximum temperature, dotted lines ·············· represent daily minimum temperature, and dash-dot lines –··–·· represent accumulated GDD.

Frequency of Plants to Joint

All unvernalized and vernalized Centennial and Centennial related plants reached the joint stage (one reproductive node) by the end of the experiment (Table 3.2). Similarly, all Madsen and Madsen related plants vernalized for 7 and 8-wk jointed by the end of the experiment (Table 3.2). Within the range of 6-6.5-wk vernalization, 100% of Madsen plants jointed, and the frequency of Madsen related plants to reach the joint stage varied between 80-100%. The trend was similar for plants exposed to 5-wk vernalization, however, even more of the jointed goatgrass by Madsen plants failed to joint when vernalized for 5-wk at 4 C. Vernalization temperature differentially affected the success of plants vernalized 4-wk to reach the joint stage. Greater than 80% of Madsen plants vernalized at 7 and 10 C jointed, while Madsen by jointed goatgrass plants consistently jointed when vernalized at all temperatures, and jointed goatgrass by Madsen plants consistently jointed only when vernalized at 7 C. The minimum vernalization treatment for any Madsen plant to joint by the end of the experiment was 2-wk at 4 C (56 VD), for any Madsen by jointed goatgrass plant was 2-wk at 7 C (98 VD), and for any jointed goatgrass by Madsen plant was 4-wk at 4 C (112 VD).

Frequency of Plants to Anthesis

All unvernalized and vernalized Centennial and Centennial related plants that jointed also reached anthesis by the end of the experiment (Table 3.3). All jointed Madsen plants reached anthesis when vernalized for 6-wk or longer (Table 3.3). Greater than 80% of Madsen plants reached anthesis when vernalized for 5-wk at all temperatures, and when vernalized for 4-wk at 7 and 10 C. Madsen plants vernalized for 4-wk at 4 C or for shorter durations did not reach the anthesis stage. Greater than 80% of Madsen by jointed goatgrass plants reached the anthesis stage when vernalized for 4-wk at 7 C and 10 C and for longer durations. In contrast, jointed goatgrass by Madsen plants required 6-wk vernalization at 7 and 10 C for greater than 80% of these plants to reach anthesis, and exposure to 7-wk vernalization at 4 C and shorter durations did not consistently vernalize these plants. Although the frequency of jointed goatgrass by Madsen plants to reach anthesis generally declined with 6-wk vernalization at 4 C and shorter durations, 100% of these plants reached the anthesis stage when vernalized for 5-wk at 7 C.

Table 3.2. Number of plants to reach the joint stage at the conclusion of the experiment out of the number of plants grown by vernalization treatment.

			Winter wheat and hybrid plants			Spring wheat and hybrid plants		
Duration	Temp[a]	VD	Mad	Mad by jgg	Jgg by Mad	Cent	Cent by jgg	Jgg by Cent
Wk	C	D * C	----------- No. plants in joint stage / No. plants grown -----------					
0	n/a	0	0/10 ¥	0/11 ¥	0/10 ¥	9/9	12/12	10/10
2	4	56	2/10 ¥	0/9 ¥	0/9 ¥	8/8	11/11	7/7
2	7	98	4/5	3/6 ¥	0/9 ¥	5/5	11/11	10/10
2	10	140	3/10 ¥	0/10 ¥	0/8 ¥	10/10	10/10	9/9
4	4	112	4/9 ¥	6/7	2/10 ¥	10/10	11/11	9/9
4	7	196	9/10	5/5	9/10	11/11	11/11	10/10
4	10	280	10/10	9/11	3/7 ¥	11/11	10/10	11/11
5	4	140	10/10	7/7	3/10 ¥	11/11	9/9	8/8
5	7	245	11/11	11/11	10/10	11/11	10/10	11/11
5	10	350	11/11	5/5	8/8	11/11	11/11	8/8
6	4	168	10/10	8/8	4/5	10/10	10/10	8/8
6	7	294	10/10	8/8	9/9	11/11	11/11	10/10
6	10	420	10/10	10/11	7/7	11/11	8/8	9/9
6.5	4	182	9/9	9/9	8/8	10/10	8/8	7/7
6.5	7	318.5	8/8	10/10	8/8	11/11	10/10	8/8
6.5	10	455	10/10	10/10	9/10	8/8	10/10	8/8
7	4	196	10/10	9/9	8/8	10/10	9/9	8/8
7	7	343	9/9	11/11	11/11	11/11	10/10	10/10
7	10	490	10/10	11/11	9/9	10/10	10/10	10/10
8	4	224	9/9	9/9	3/3	11/11	11/11	6/6
8	7	392	10/10	11/11	9/9	9/9	9/9	4/4
8	10	560	10/10	12/12	6/6	9/9	9/9	9/9

¥ Vernalization treatments by plant type where the frequency of plants to joint was less than 80%.

[a] Abbreviations: Temp=temperature; VD=vernalization days; Mad=Madsen cultivar winter wheat; Jgg=jointed goatgrass; and Cent=Centennial cultivar spring wheat.

Accelerated Reproductive Development

Vernalization treatments did not accelerate the reproductive development of Centennial spring wheat plants (Fig. 3.2). Unvernalized Centennial plants reached the joint stage after approximately 700 GDD in the greenhouse, plants vernalized for 8-wk reached the joint stage after a similar period, and there were no differences among vernalization temperatures (Table 3.4). Vernalization duration, but not temperature, affected the reproductive development of both Centennial hybrid types (Table 3.4). Unvernalized spring type hybrid plants required 28-44 more GDD (approximately 1.6 d) to reach the joint stage than similar plants vernalized for 2-wk or longer (Fig. 3.2). Although statistically significant, the accelerated reproductive development of spring type hybrid plants in response to 2-wk vernalization is small. More importantly, reciprocal crosses between spring wheat and jointed goatgrass produced hybrid plants that were nearly insensitive to vernalization. A vernalization insensitive hybrid might serve as a one-step bridge for gene flow of the dominant *Vrn-1* spring habit allele (Brule-Babel and Fowler 1988) from spring wheat into jointed goatgrass populations. Several wheat D genome alleles persisted in BC_1 and BC_2 generations produced with jointed goatgrass as the recurrent pollen donor after an original cross between wheat and jointed goatgrass (Kroiss et al., 2004).

Table 3.3. Number of plants to reach the anthesis stage at the conclusion of the experiment out of the number of plants to reach the joint stage by vernalization treatment.

			Winter wheat and hybrid plants			Spring wheat and hybrid plants		
Duration	Temp[a]	VD	Mad	Mad by jgg	Jgg by Mad	Cent	Cent by jgg	Jgg by Cent
Wk	C	Days * C	---- No. plants in anthesis stage / No. plants to reach joint stage ----					
0	n/a	0	n/a	n/a	n/a	9/9	12/12	10/10
2	4	56	0/2 ¥	n/a	n/a	8/8	11/11	7/7
2	7	98	0/4 ¥	0/3 ¥	n/a	5/5	11/11	10/10
2	10	140	0/3 ¥	n/a	n/a	10/10	10/10	9/9
4	4	112	0/4 ¥	2/6 ¥	0/2 ¥	10/10	11/11	9/9
4	7	196	8/9	5/5	1/9 ¥	11/11	11/11	10/10
4	10	280	9/10	8/9	1/3 ¥	11/11	10/10	11/11
5	4	140	10/10	7/7	1/3 ¥	11/11	9/9	8/8
5	7	245	9/11	11/11	10/10	11/11	10/10	11/11
5	10	350	10/11	5/5	5/8 ¥	11/11	11/11	8/8
6	4	168	10/10	8/8	3/4 ¥	10/10	10/10	8/8
6	7	294	10/10	8/8	8/9	11/11	11/11	10/10
6	10	420	10/10	10/10	7/7	11/11	8/8	9/9
6.5	4	182	9/9	9/9	8/8	10/10	8/8	7/7
6.5	7	318.5	8/8	10/10	8/8	11/11	10/10	8/8
6.5	10	455	10/10	9/10	9/9	8/8	10/10	8/8
7	4	196	10/10	8/9	8/8	10/10	9/9	8/8
7	7	343	9/9	11/11	11/11	11/11	10/10	10/10
7	10	490	10/10	10/11	9/9	10/10	10/10	10/10
8	4	224	9/9	9/9	3/3	11/11	11/11	6/6
8	7	392	10/10	9/11	8/9	9/9	9/9	4/4
8	10	560	10/10	11/12	6/6	9/9	9/9	9/9

¥ Vernalization treatments by plant type where the frequency of jointed plants to reach the anthesis stage was less than 80%.

[a] Abbreviations: Temp=temperature; VD=vernalization days; Mad=Madsen cultivar winter wheat; Jgg=jointed goatgrass; and Cent=Centennial cultivar spring wheat.

Vernalization treatments accelerated the reproductive development of Madsen and Madsen related plants, and responses were unique for each plant type (Fig. 3.3). However, all Madsen and Madsen related plants vernalized for 8-wk jointed after 718-

919 GDD in the greenhouse (Table 3.4), and these values were within the expected range for wheat to joint (Cook et al., 1994). Vernalization duration ($F_{1,173}$=414.56; p<0.0001) and temperature ($F_{2,173}$=4.18; p=0.0168), but not their interaction, affected the reproductive development of Madsen plants. Models predicted that unvernalized Madsen plants would have jointed after 2087-2363 GDD in the greenhouse – values that are near the ranges for the end of the experiment. Madsen plants vernalized for 2-wk reached the joint stage after 1839 GDD when vernalized at 4 C, after 1804 GDD when vernalized at 7 C, and after 1697 GDD when vernalized at 10 C. Each additional week of vernalization resulted in Madsen plants reaching the joint stage 195-262 GDD (8-11 d) earlier than shorter durations (Table 3.4).

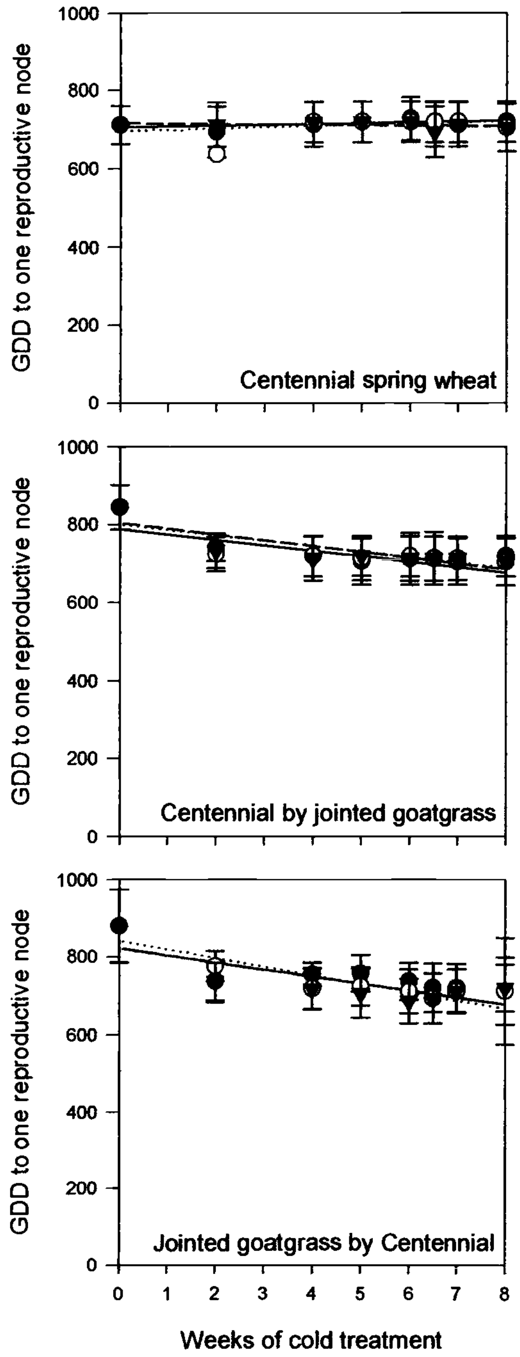

Figure 3.2. Effect of vernalization duration and temperature on the time in growing degree days (GDD) from the end of the vernalization treatment to the joint stage (one reproductive node) for Centennial and Centennial related plants. Solid lines and closed circles —●— represent actual and predicted values for plants vernalized at 4 C, dotted lines and open circles ····○···· represent 7 C, and dashed lines and closed triangles - -▼- - represent 10 C.

Table 3.4. Equations for the predicted GDD to joint by plant type and vernalization temperature as a function of vernalization duration. Confidence intervals (α=0.05) for equation intercepts and slopes are shown in parenthesis. Mean values and confidence intervals for actual GDD to joint after 8-wk vernalization are provided.

	Temperature					
	4 C		7 C		10 C	
Plant type	Equation	8-wk actual	Equation	8-wk actual	Equation	8-wk actual
Mad[a]	2363(255)-262(43)*week	728(56)	2244(209)-220(35)*week	719(530)	2087(217)-195(36)*week	719(530)
Mad by jgg	2658(256)-278(42)*week	727(49)	2254(196)-207(31)*week	731(46)	1961(238)-165(37)*week	718(47)
Jgg by Mad	3005(466)-289(76)*week	919(345)	2722(260)-257(42)*week	797(97)	2745(358)-266(56)*week	748(67)
Cent	706(36)+2(7)*week	719(53)	697(39)+3(7)*week	704(61)	716(37)-1(7)*week	704(61)
Cent by jgg	788(35)-14(7)*week	719(53)	800(37)-14(7)*week	704(61)	804(37)-15(7)*week	704(61)
Jgg by Cent	822(43)-18(9)*week	712(86)	842(43)-22(8)*week	712(138)	822(43)-18(8)*week	721(61)

[a] Abbreviations: Mad=Madsen cultivar winter wheat; Jgg=jointed goatgrass; and Cent=Centennial cultivar spring wheat.

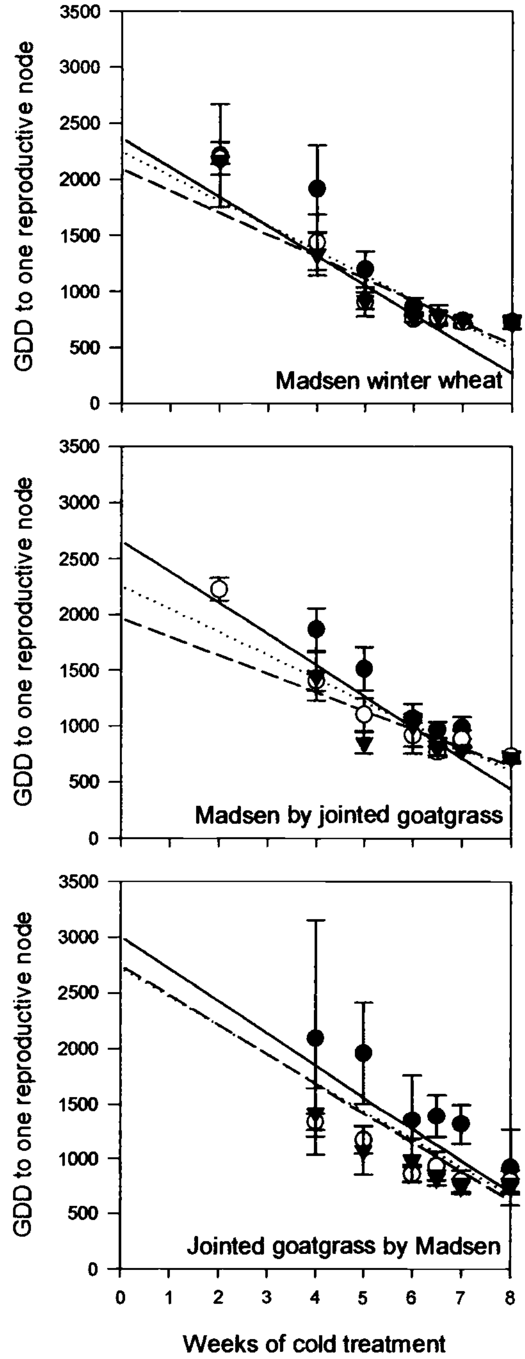

Figure 3.3. Effect of vernalization duration and temperature on the time in growing degree days (GDD) from the end of the vernalization treatment to the joint stage (one reproductive node) for Madsen and Madsen related plants. Solid lines and closed circles —●— represent actual and predicted values for plants vernalized at 4 C, dotted lines and open circles ·····○····· represent 7 C, and dashed lines and closed triangles --▼-- represent 10 C.

The main effects of vernalization duration and temperature, and their interaction ($F_{2,158}$=7.97; p=0.0005), affected the reproductive development of Madsen by jointed goatgrass plants. Madsen by jointed goatgrass plants vernalized for 2-wk at 7 C jointed, but similar plants vernalized at 4 and 10 C did not joint by the end of the experiment (Fig. 3.3). Furthermore, the vernalization response over the duration of the experiment was strongest for plants vernalized at 4 C. Each additional weekly increase in vernalization duration resulted in these plants jointing 165 GDD (7.4 d) earlier when vernalized at 10 C, 207 GDD (9.3 d) earlier when vernalized at 7 C, and 278 GDD (12.5 d) earlier when vernalized at 4 C (Table 3.4). In contrast, vernalization duration, but not temperature, affected the reproductive development of jointed goatgrass by Madsen plants. Models predicted that unvernalized jointed goatgrass by Madsen plants would joint after 2722-3005 GDD in the greenhouse (Table 3.4); values that were beyond the ranges of the experiment. Each additional weekly increase in vernalization duration resulted in these plants jointing 257-289 GDD (11.5-13.0 d) earlier than shorter vernalization durations.

Tiller Number per Plant

The main effect of vernalization duration, but not temperature, affected tiller production in Centennial and Centennial by jointed goatgrass plants. Subsequently, tiller production numbers for Centennial and Centennial by jointed goatgrass plants vernalized 0, 4, and 8-wk were averaged over temperature and regressed against GDD in the final model. Tiller number per Centennial and Centennial by jointed goatgrass plants increased with GDD (Fig. 3.4). The main effects of GDD and vernalization duration affected the number of tillers produced by Centennial plants. Plants vernalized for 8-wk produced a total of 1.2 tillers by harvest, while unvernalized plants produced 1.8 tillers by the end of the experiment. Centennial plants produced one tiller for every 1000 accumulated GDD (Table 3.5), and this response was consistent across vernalization durations. Because the onset to reproductive development of Centennial plants occurred rapidly, it is hypothesized that final tiller production numbers were limited by the cool temperatures experienced by vernalized plants, or promoted by warm temperatures exposed to unvernalized plants.

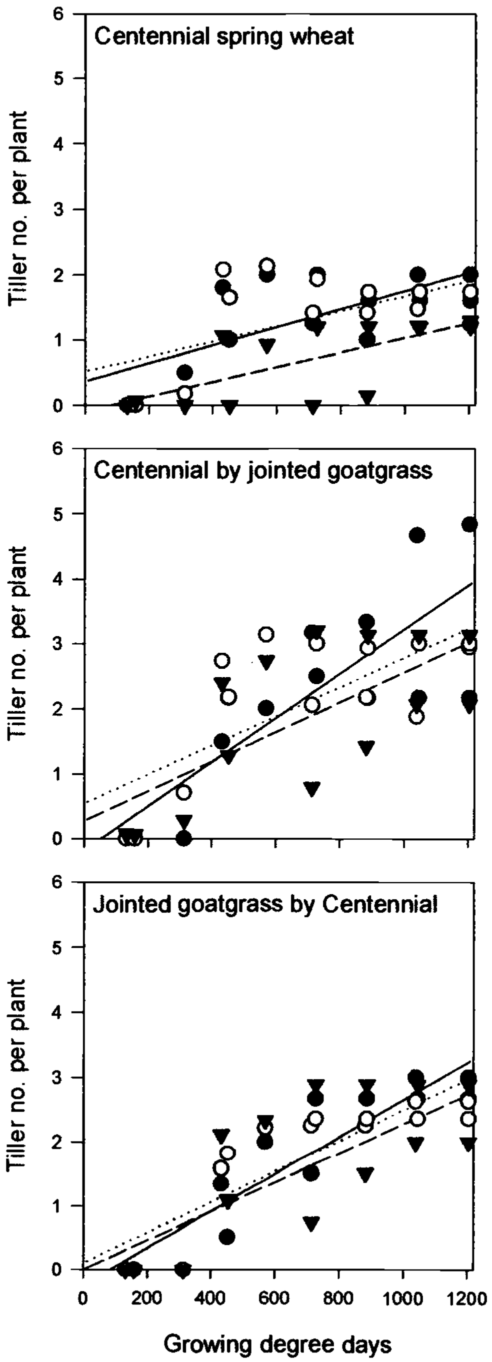

Figure 3.4. Effect of 0, 4, and 8-wk vernalization on the total number of tillers per Centennial and Centennial related hybrid plants as a function of time in growing degree days (GDD). Solid circles and lines —●— represent actual and predicted values for the responses of plants vernalized 0-wk, dotted lines and open circles ·····○····· represent 4-wk vernalization, and dashed lines and closed triangles - -▼- - represent 8-wk vernalization. Responses were averaged over vernalization temperature.

Table 3.5. Equations for the predicted tiller production by plant type and vernalization duration as a function of GDD. Confidence intervals (α=0.05) for equation intercepts are provided in parenthesis.

	Vernalization duration											
	0-wk				4-wk				8-wk			
Plant type	Intercept	Slope	Lower CI[a]	Upper CI	Intercept	Slope	Lower CI	Upper CI	Intercept	Slope	Lower CI	Upper CI
Mad	0.19(0.41)	0.002	0.002	0.003	0.66(0.25)	0.001	0.001	0.001	0.76(0.25)	0.000	0.000	0.000
Mad by jgg	-2.53(0.78)	0.007	0.007	0.008	0.28(0.54)	0.004	0.004	0.004	0.92(0.46)	0.001	0.001	0.002
Jgg by Mad	-3.31(0.78)	0.009	0.008	0.009	-1.93(0.47)	0.007	0.006	0.007	-0.27(0.58)	0.003	0.003	0.004
Cent	0.36(0.47)	0.001	0.001	0.002	0.51(0.25)	0.001	0.001	0.001	-0.09(0.26)	0.001	0.001	0.001
Cent by jgg	-0.18(0.51)	0.003	0.003	0.004	0.54(0.31)	0.002	0.002	0.003	0.27(0.33)	0.002	0.002	0.003
Jgg by Cent	-0.24(0.44)	0.003	0.002	0.003	0.10(0.25)	0.002	0.002	0.003	0.00(0.30)	0.002	0.002	0.003

[a] Abbreviations: CI=confidence interval; Mad=Madsen cultivar winter wheat; Jgg=jointed goatgrass; and Cent=Centennial cultivar spring wheat.

The main effects of GDD and vernalization duration, and their interaction, affected the number of tillers produced by Centennial by jointed goatgrass plants (Fig. 3.4). Unvernalized Centennial by jointed goatgrass plants initially produced fewer tillers than vernalized plants, but by the experiment's conclusion, unvernalized plants produced 3.5 tillers per plant compared to 3.0 tillers per plant for plants vernalized 4-wk and 2.6 tillers per plant for plants vernalized 8-wk. Unvernalized plants produced three tillers for every accumulated 1000 GDD, while 4 and 8-wk vernalized plants produced only two tillers under the same conditions (Table 3.5). Neither vernalization duration, nor temperature affected tiller production in jointed goatgrass by Centennial plants. The rate of tiller production as a function of GDD in jointed goatgrass by Centennial plants was similar across all vernalization durations ($F_{2,421}$=0.88; p=0.4149), and these plants produced 2-3 tillers for every 1000 accumulated GDD. The complex interactions between vernalization effects, genetic contributions for prolific tillering in jointed goatgrass, and male sterility that extends the vegetative period likely contributed to differential tillering responses among Centennial and Centennial related hybrid plants.

The main effects of vernalization duration and temperature influenced tiller production in Madsen plants. The effect of temperature was approximately one-third the effect of vernalization duration ($F_{1,977}$=34.09 for temperature; $F_{1,977}$=88.14 for duration), and to simplify comparison with spring type plants, tiller production numbers averaged over temperature were regressed against GDD in the final models for Madsen plants vernalized 0, 4, and 8-wk. Tiller production increased with GDD in Madsen plants (Fig. 3.5). The main effects of GDD and vernalization duration, and their interaction, affected tiller production. Unvernalized Madsen plants initially produced fewer tillers than vernalized plants, but by the end of the experiment, unvernalized plants produced 5.6 tillers per plant compared to 2.2 tillers per plant for plants vernalized 4-wk, and 1.1 tillers per plant for plants vernalized 8-wk (Fig. 3.5). Plant age might account for different tiller numbers during the early periods in the greenhouse, and explain the interaction between GDD and vernalization. Differences in final tiller numbers and rates of tiller production for vernalized plants confirm sensitivity of these plants to vernalization (Chouard 1960).

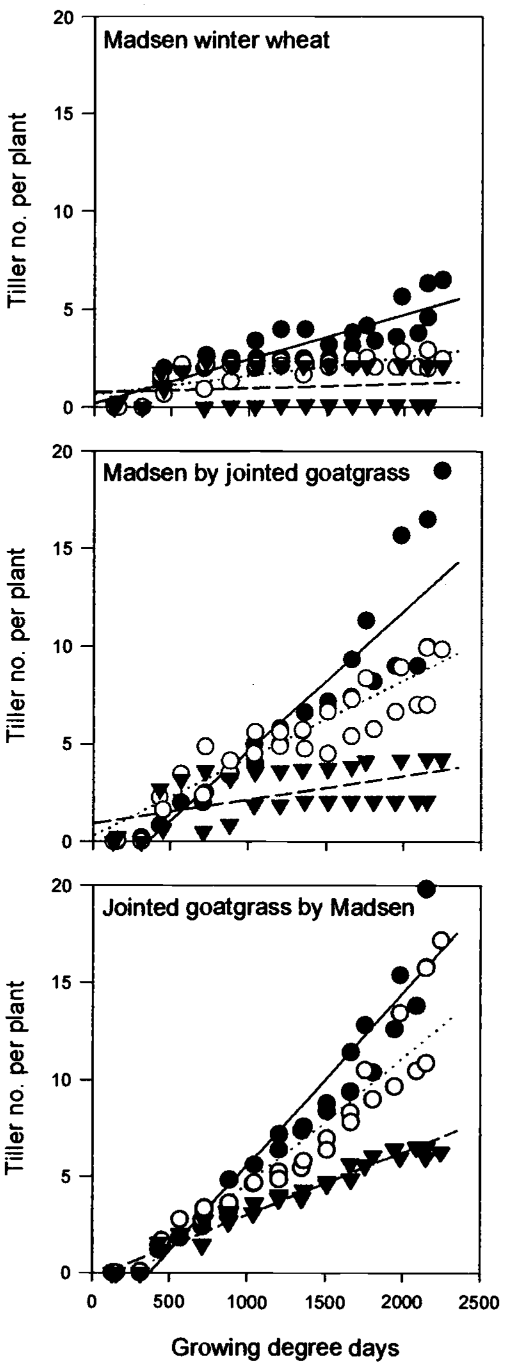

Figure 3.5. Effect of 0, 4, and 8-wk vernalization on the total number of tillers per Madsen and Madsen related hybrid plants as a function of time in growing degree days (GDD). Solid circles and lines —●— represent actual and predicted values for the responses of plants vernalized 0-wk, dotted lines and open circles ···○··· represent 4-wk vernalization, and dashed lines and closed triangles --▼-- represent 8-wk vernalization. Responses were averaged over vernalization temperature.

Vernalization duration, temperature, and their interaction affected tiller production in Madsen by jointed goatgrass plants. However, the effect of duration was approximately 100 times more influential than temperature (data not shown.) Data were averaged over temperature and re-analyzed as previously described. GDD, vernalization duration, and their interaction influenced tiller production in Madsen by jointed goatgrass plants (Fig. 3.5). Similar to other plant types, fewer tillers on younger, unvernalized plants in the early portion of the experiment might explain these observations. Unvernalized Madsen by jointed goatgrass plants produced seven tillers for every accumulated 1000 GDD, while 4 and 8-wk vernalized plants produced four tillers and one tiller, respectively, over a similar period (Table 3.5). These results were observed also in the growth of jointed goatgrass by Madsen plants. In summary, both winter type hybrid plants exposed to 0, 4, and 8-wk vernalization produced more tillers than similarly treated Madsen plants. For an explanation, the reader is referred to the paragraph on tiller production in spring type hybrid plants (see above).

Proportion of Reproductive Tillers

Although all Centennial plants reached anthesis by the end of the experiment, vernalization duration affected the proportion of reproductive tillers produced. These results are in agreement with Flood and Halloran (1986) who defined that spring type plants may respond to vernalization with little accelerated floral development. Plants that were subjected to 2-wk vernalization, or 4-wk vernalization at 10 C and longer vernalization periods, had a consistently higher proportion of reproductive tillers compared to unvernalized plants and plants vernalized for 4-wk at 4 and 7 C (Table 3.6). The production of reproductive tillers varied in Centennial related hybrid plants such that unvernalized plants and plants vernalized for 8-wk at 10 C produced the same percentages of reproductive tillers. Because Centennial and Centennial related hybrid plants often produced three tillers or fewer, a one unit change in reproductive and non-reproductive tiller numbers reflected a proportionally greater significance in the analysis compared to plant types with more tillers. A more conservative data interpretation might infer that vernalization duration did not affect the proportion of reproductive tillers produced by Centennial and Centennial related plants.

Vernalization affected the proportion of reproductive tillers produced by Madsen plants. Madsen plants subjected to 4-wk vernalization at 7 and 10 C and for longer periods produced greater proportions of reproductive tillers than unvernalized and 2-wk vernalized plants, while Madsen related hybrid plants required 5-wk vernalization at 7 C for the same biological result (Table 3.6). These results clarify the vernalization requirements of Madsen and Madsen related hybrids within the ranges predicted by jointing and anthesis frequency charts, and they represent the minimum environmental conditions necessary to shift growth from a vegetative (accumulating tillers) to reproductive stage (accumulating spikes).

Seed Germination

Centennial seed germination was not affected by vernalization. For all vernalization treatments, seed germination values ranged from 98-100% (Table 3.7). The minimum vernalization treatment required to produce germinable Madsen seed was 4-wk vernalization at 7 C. Although this germination value was the first in the treatment series to be different from 0, it was also similar to 100%. The production of germinable seed by Madsen plants exposed to a minimum vernalization treatment is likely the result of selection by winter wheat breeders for rapid and consistent seed development.

Table 3.6. Percentage of reproductive tillers produced per plant type at the conclusion of the experiment by vernalization treatment. Mean values and 95% confidence intervals in parenthesis are presented.

			Winter wheat and hybrid plants			Spring wheat and hybrid plants		
Duration	Temp[a]	VD	Madsen	Mad by jgg	Jgg by Mad	Cent	Cent by jgg	Jgg by Cent
Wk	C	Days * C	------------------------ Reproductive tillers % ------------------------					
0	n/a	0	n/a	n/a	n/a	54(12.2)	63(12.9)	51(13.3)
2	4	56	n/a	n/a	n/a	81(13.0)	79(13.4)	78(15.9)
2	7	98	n/a	n/a	n/a	90(16.4)	64(13.4)	67(13.3)
2	10	140	n/a	n/a	n/a	100(11.6)	73(14.1)	79(14.0)
4	4	112	n/a	3(19.4)	n/a	58(11.6)	68(18.2)	65(14.0)
4	7	196	31(11.2) ¥	23(22.9)	19(15.3)	62(11.1)	75(13.4)	81(13.3)
4	10	280	50(11.2)	36(15.5)	4(18.3)	73(11.1) ¥	86(14.1)	88(12.7)
5	4	140	77(11.2)	18(19.4)	1(15.3)	97(11.1)	87(14.8)	95(14.9)
5	7	245	92(10.7)	53(15.5) ¥	54(14.6) ¥	100(11.1)	88(14.1)	86(12.7)
5	10	350	91(10.7)	54(22.9)	24(17.1)	100(11.1)	74(13.4)	85(14.9)
6	4	168	95(11.2)	45(18.1)	42(19.8)	97(11.6)	76(14.1)	93(14.9)
6	7	294	100(11.2)	65(18.1)	72(16.1)	92(11.1)	91(13.4)	94(13.3)
6	10	420	100(11.2)	53(15.5)	59(18.3)	97(11.1)	84(15.7)	93(14.0)
6.5	4	182	94(11.8)	56(17.1)	49(17.1)	97(11.1)	93(15.7)	67(15.9)
6.5	7	318.5	100(12.6)	74(16.2)	71(17.1)	92(11.1)	95(14.1)	74(14.9)
6.5	10	455	100(11.2)	78(16.2)	39(15.3)	96(13.0)	91(14.1)	73(14.9)
7	4	196	75(11.2)	47(15.5)	38(17.1)	100(11.6)	91(14.8)	72(14.9)
7	7	343	93(11.8)	66(15.5)	63(14.6)	94(11.1)	87(14.1)	81(13.3)
7	10	490	100(11.2)	68(15.5)	49(16.1)	85(11.6)	81(14.1)	84(13.3)
8	4	224	74(11.8)	75(17.1)	47(27.9)	73(11.1)	67(13.4)	72(17.2)
8	7	392	72(11.2)	64(15.5)	35(16.1)	80(12.2)	76(14.8)	73(21.1) ¥
8	10	560	65(11.2)	89(14.8)	69(19.8)	74(12.2)	55(14.8)	84(14.0)

¥ The minimum treatment for each plant type to produce reproductive tillers at numbers greater than 0 or greater than unvernalized plants. A condition of the ¥ is that every duration or temperature treatment greater than the minimum must increase also the percentage of reproductive tillers produced compared to the control.

[a] Abbreviations: Temp=temperature; VD=vernalization days; Mad=Madsen cultivar winter wheat; Jgg=jointed goatgrass; Cent=Centennial cultivar spring wheat.

Table 3.7. Percent seed germination by plant type and vernalization treatment. Mean values and 95% confidence intervals in parenthesis are presented.

			Wheat	
Duration	Temp[a]	VD	Mad	Cent
Wk	C	Days * C	-- Germination % --	
0	n/a	0	0(0.0)	100(0.0)
2	4	56	0(0.0)	100(0.0)
2	7	98	0(0.0)	100(0.0)
2	10	140	0(0.0)	100(0.0)
4	4	112	10(22.6)	100(0.0)
4	7	196	80(30.1) ¥	100(0.0)
4	10	280	90(22.6)	100(0.0)
5	4	140	100(0.0)	100(0.0)
5	7	245	99(1.2)	100(0.0)
5	10	350	99(0.4)	100(0.0)
6	4	168	98(2.4)	100(0.0)
6	7	294	99(0.5)	100(0.0)
6	10	420	98(1.6)	98(1.5)
6.5	4	182	100(0.0)	100(0.0)
6.5	7	318.5	100(0.0)	100(0.0)
6.5	10	455	97(6.4)	100(0.0)
7	4	196	100(0.0)	99(1.1)
7	7	343	99(1.5)	100(0.0)
7	10	490	99(1.0)	100(0.0)
8	4	224	100(0.0)	100(0.0)
8	7	392	100(0.0)	100(0.0)
8	10	560	100(0.0)	99(0.7)

¥ denotes the minimum treatment for each plant type to produce germinable seed. A condition of the ¥ is that every duration or temperature treatment greater than the minimum must also produce germinable seed.

[a] Abbreviations: Temp=temperature; VD=vernalization days; Mad=Madsen cultivar winter wheat; Cent=Centennial cultivar spring wheat.

CONCLUSIONS

The linear calculation of vernalization days to quantify the degree of vernalization experienced by these plants inadequately modeled plant growth and reproductive development. For many biological responses and plant types, a significant interaction between vernalization duration and temperature revealed that these conditions were not equally affecting plant growth and reproductive development. Interpretation was complicated further by the different ages of the plants used in these studies, although this factor should be recognized as a compromise for growing plants under the same conditions in the greenhouse. No single temperature was shown to be the most effective as a vernalization treatment, and minimum vernalization durations were identified for vernalization sensitive plant types.

Gene flow from wheat to jointed goatgrass is a risk associated with the development and release of herbicide-resistant wheat cultivars. In traditional wheat cropping systems, other wheat genes, such as for spring type habit, or insect and pathogen resistance might also migrate into jointed goatgrass populations, and increase the adaptability of jointed goatgrass to grow competitively and successfully under stressful environmental conditions. Reciprocal crosses between spring wheat and jointed goatgrass produced hybrid plants that were nearly insensitive to vernalization. These events document an increased potential for the transfer of spring type alleles into jointed goatgrass populations. Because jointed goatgrass is not as dependent on vernalization for reproduction as winter wheat (Walenta et al., 2002), and spring wheat and jointed goatgrass have been observed nicking during anthesis in Oregon fields (Morrison et al., 2002), spring cropped fields should be monitored for the presence of wheat by jointed goatgrass hybrid plants, and these plants removed before seed production and dissemination.

Synchronous reproductive development between Madsen and Madsen by jointed goatgrass plants in response to varying vernalization conditions increases the risks involved for the transfer of wheat genes into jointed goatgrass populations. The similar frequencies with which Madsen and Madsen by jointed goatgrass plants reached anthesis confirmed these responses. Jointed goatgrass by Madsen plants exhibited more variability in their reproductive development responses to varying vernalization conditions, and the frequencies of these plants to reach anthesis were fewer than Madsen plants and reciprocal hybrid plants. Because pollination in hybridization dynamics occurs primarily in the direction of crop to weed (Ladizinsky 1985), subsequent backcross generations may progressively lose jointed goatgrass genes, and return to a wheat-type plant. However, a low possibility of backcrossing to jointed goatgrass exists (Seefeldt et al., 1998) and partial self-fertility was restored after two backcross generations (Wang et al., 2001).

The most effective method to consistently reduce the risks of gene movement from crop to weed is to remove hybrid and backcross generations from the field (Wang et al., 2001). Wheat by jointed goatgrass hybrid plants are distinguished visually from wheat and jointed goatgrass plants, and should be removed with regular scouting. Furthermore, only certified wheat seed should be planted, because wheat seed from previous harvests might have been pollinated by jointed goatgrass. These practices reduce the risks of producing a backcross generation, indistinguishable from either parent, and necessary for the persistence of wheat genes in jointed goatgrass populations.

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CHAPTER 4

Jointed Goatgrass (*Aegilops cylindrica*) Vernalization Requirements

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Quantification of jointed goatgrass vernalization requirements is necessary to predict the conditions under which jointed goatgrass plants can establish and be available for crossing with wheat. Jointed goatgrass seedlings from five populations were exposed to 0, 2, 4, 5, 6, 6.5, 7, and 8-wk vernalization at 4, 7, and 10 C. Tiller production and reproductive growth stages were recorded for plants grown over 13 weeks in the greenhouse. Greater than 80% of jointed goatgrass plants from all populations vernalized for 6-wk or longer durations reached the joint stage by the end of the experiment. However, populations were polymorphic for reproductive response at shorter vernalization durations. A comparison of the reproductive responses revealed that plants of Washington and Oregon winter and spring type jointed goatgrass populations extended the period of time between the joint and anthesis stage such that plants of these populations jointed, but failed to reach the anthesis stage in the absence of vernalization. Conversely, plants of a Washington roadside population required a longer initial vernalization exposure to reach the joint stage, but these plants consistently reached anthesis. Jointed goatgrass populations differed in the minimum vernalization treatment required to produce reproductive tillers; WA-R plants required 6-wk vernalization at 7 C, WA-W plants required 6.5-wk at 7 C, and WA-S plants required 7-wk at 4 C. Plants from both OR populations required 7-wk vernalization at 4 C. Our results confirm the quantitative vernalization requirement of jointed goatgrass and assert polymorphism among jointed goatgrass populations for vernalization requirements. While a 6-wk vernalization duration represents the minimum requirement for synchronous reproduction among a jointed goatgrass population, Madsen winter wheat, and Madsen by jointed goatgrass hybrids, the risk of gene transfer might be greater when the onset of reproductive development is most similar - after 7-wk vernalization.

Nomenclature: Jointed goatgrass, *Aegilops cylindrica* Host, AEGCY.

Key words: Anthesis, germination, growing degree days, joint stage, reproductive node, tillers, vernalization days.

Jointed goatgrass (*Aegilops cylindrica* Host) (CD genomes) is a wild relative of domesticated bread wheat (*Triticum aestivum* L.) (ABD genomes), and a noxious weed in most winter wheat production areas of the central and western USA (Donald and Ogg 1991). Jointed goatgrass infestations reduce winter wheat yields (Fenster and Wicks 1976; Fleming et al. 1988), increase dockage penalties, reduce land values, result in lost markets, and limit crop rotation choices (Anonymous 2004). Selective jointed goatgrass control in winter wheat became possible recently through the release of wheat cultivars resistant to imazamox herbicide (Haley et al. 2003; Lazar et al. 2003). However, transfer of the herbicide-resistance gene from winter wheat to jointed goatgrass could make control of this weed even more difficult. Sexual compatibility between wheat and jointed goatgrass produces female-fertile hybrid plants (Seefeldt et al. 1998; Snyder et al. 2000; Zemetra et al. 1998) that serve as a bridge for gene flow. Subsequent backcrossing and restoration of self-fertility in these plants (Wang et al. 2001) might lead to the persistence of wheat genes in a jointed goatgrass population.

Quantification of jointed goatgrass vernalization requirements is necessary to predict the conditions under which jointed goatgrass plants can establish and be available for crossing with wheat. Vernalization is defined as the effect of chilling that corresponds to accelerated reproductive development (Chouard 1960). Exposure to low temperatures for several weeks allows plants to escape the risks of cold injury during reproductive growth (Flood and Halloran 1986), and synchronizes cereal development in response to long photoperiods (Hay and Kirby 1991; Hay and Ellis 1998). In the absence of vernalization, the vegetative period is extended, and floral initiation is delayed (Richardson et al. 1986). Winter wheat plants require approximately 4-6 wk vernalization at temperatures below 10 C to induce flowering, and are planted in the fall. Spring wheat plants are vernalization insensitive and flower without such a treatment. Several genes influence the vernalization requirement; homozygous recessive alleles at the *vrn-A1*, *vrn-B1*, and *vrn-D1* loci result in a winter habit, and spring habit is conferred by a dominant allele at any of the three loci (McIntosh et al. 2003).

Jointed goatgrass has a versatile biology that allows it to either complete its life cycle rapidly or to prolong it under conditions of favorable moisture, light and temperature. Donald (1984) studied the growth responses of a single jointed goatgrass population vernalized at 3 ± 2 C for 2-wk intervals over 8-wk, and reported that the low temperature treatment modified maturation and flowering biology in the greenhouse. Plants vernalized for 8-wk headed approximately 10-wk earlier than unvernalized plants, and vernalized plants formed more spikes per plant and accumulated more dry weight per spike than unvernalized plants. Unvernalized jointed goatgrass plants flowered after 160-250 d in the greenhouse, and Donald concluded that the winter annual reproductive biology of jointed goatgrass was more facultative than obligate. Efforts to model the reproductive success of jointed goatgrass could be improved with vernalization studies using several jointed goatgrass populations and a range of vernalization temperatures.

Integrated management strategies for several winter wheat production regions have been recommended for jointed goatgrass control (Evans et al. 1999; Pester et al. 1999; Young et al. 2002). Cultural control methods that might reduce the severity of a jointed goatgrass infestation include rotations with winter wheat grown once every 3-4 yr (Donald and Ogg 1991), and rotation to spring crops (Veseth 1988). Tillage and herbicide applications in preparation and maintenance of spring crops remove fall and early-spring germinating jointed goatgrass. However, jointed goatgrass vernalization requirements are not understood well enough to evaluate the success of a spring cropping regime as a control measure or to guarantee against gene introgression from spring wheat into jointed goatgrass. Furthermore, if spring cropping regimes were to become a successful alternative to the traditional winter wheat system, this change might select for a vernalization insensitive jointed goatgrass biotype. Walenta et al. (2002) found no differences in vernalization responses between spring and winter jointed goatgrass cohorts collected from a field in its first year of spring cereal production. Testing for the selection of spring jointed goatgrass biotypes could be improved using jointed goatgrass populations from fields with several years history of annual spring cropping.

The objective of this research was to quantify the phenology and reproductive development of five jointed goatgrass populations in response to varying vernalization conditions.

Materials and Methods

Mature spikelets of five jointed goatgrass populations were collected in the summer of 2001 from a roadside, a winter wheat field, and a spring wheat field in south central Washington, and from a winter wheat field and spring wheat field in eastern Oregon (Table 4.1). 'Winter' jointed goatgrass populations were collected in fields with a continuous history of winter wheat/fallow crop rotation, while 'spring' populations were collected in fields with histories of at least 5 yr continuous spring cropping. The history of the roadside population was not confirmed. Mature spikes were clipped from the plants when the culms appeared dry – at or near the time of winter wheat harvest for each location. Samples were cleaned by hand to remove culms and debris, and stored dry at room temperature (22 ± 2 C) until use.

Table 4.1. Descriptions of jointed goatgrass populations collected in 2001 and used in greenhouse vernalization experiments.

Population	Habitat/type	Elevation ---- m ----	Latitude ---- ° N ----	Longitude ---- ° W ----
Bickleton, WA – R	Roadside/unknown	920	46.00	120.30
Bickleton, WA – W	Crop/winter	920	46.00	120.30
Bickleton, WA – S	Crop/spring	920	46.00	120.30
Helix, OR – W	Crop/winter	535	45.85	118.65
Helix, OR – S	Crop/spring	535	45.85	118.65

The five jointed goatgrass populations were grown during the 2001-02 season in a common garden nursery at the Columbia Basin Agricultural Research Center in Pendleton, Oregon. The nursery site was selected from an area with no previous jointed goatgrass infestations. Jointed goatgrass spikelets (*n*=45) from each population were sown 3 cm deep into 2-m rows spaced 60 cm apart. Thirty g of slow-release, granular fertilizer[1] was evenly scattered down the furrow at planting. The site was weeded by hand as necessary and no other maintenance was required. At maturity, intact spikes from each jointed goatgrass population were harvested by hand, cleaned, and stored as previously described.

Spikelets from each population were placed on two 10.2 by 10.2 cm germination blotters[2] wetted with 25 ml deionized water in similarly sized germination boxes[3]. Spikelets were incubated at 25/15 C day/night temperatures in the dark for two d. Six germinated spikelets with consistent radicle lengths were sown 2 cm deep into 3.8-cm diam by 14-cm depth cones[4] filled with potting soil[5]. Cones were placed inside trays for easy transport, and trays arranged randomly into growth chambers set to constant 4, 7, and 10 C temperatures and 8-h photoperiod. Seedlings were exposed to 0, 2, 4, 5, 6, 6.5, 7, and 8-wk vernalization. Vernalization durations were scheduled so that all plants completed the vernalization treatment on the same calendar date. After the vernalization treatment, but before transferring to the greenhouse, temperatures in all growth chambers were set to 10 C for 2 d. Temperatures were raised 5 C over the next 5 d in an acclimation period. Plants were moved into a greenhouse set to 30/18 C day/night temperatures and 16-h photoperiod. Trays were rearranged randomly each week in both environments to minimize the variation attributed to neighboring fans and lights. Plants were watered when the soil surface appeared dry, and a water-soluble fertilizer[6] was applied at labeled rates weekly during both phases of these studies. Plants in the greenhouse were monitored weekly for pests, and sprayed with nicotine[7] at labeled rates as necessary.

Phenological measurements were collected beginning with the transfer of plants into the greenhouse; tiller number per plant was recorded weekly for plants exposed to 0, 4, and 8-wk vernalization, and growth stages on all plants were recorded twice a week. Days from the end of the vernalization period to jointing stage, awn emergence from the boot, full spike emergence from the boot, and the first day of anthesis were also recorded. Approximately 13 weeks after plants were transferred to the greenhouse, all plants were scored as headed or not headed. Vegetative and reproductive tillers were counted. Spikes were clipped from the culms and stored in the dark at 22 ± 2 C for later use in germination studies. Approximately three weeks after harvest, germination assays were conducted on jointed goatgrass spikelets incubated at 25/15 C day/night temperatures and 12-h photoperiod over 14 d. Germination was defined as the presence of 5-mm radicle. The experiment was repeated.

Greenhouse minimum and maximum temperatures were recorded daily. Growing degree days (GDD) were calculated using a base temperature of 0 C subtracted from the daily average air temperature (C). Accumulated GDD were summed beginning with the acclimation period in the growth chamber and ending with harvest in the greenhouse.

Vernalization days (VD) were calculated as the product of the vernalization temperature and days exposed for a given treatment (Table 4.2). Two vernalization temperature by duration treatments resulted in the same net accumulated vernalization days – 2-wk at 10 C was identical to 5-wk at 4 C, and 4-wk at 7 C was identical to 7-wk at 4 C.

Table 4.2. Accumulated vernalization days (VD) by vernalization duration and temperature.

Duration		Temperature		
		4 C	7 C	10 C
Weeks	Days		VD	
0	0	0	0	0
2	14	56	98	140
4	28	112	196	280
5	35	140	245	350
6	42	168	294	420
6.5	45.5	182	318.5	455
7	49	196	343	490
8	56	224	392	560

The GDD number from acclimation to the joint stage plotted against VD showed negative, linear relationships, and suggested that differences between durations and temperatures existed for all jointed goatgrass populations. Jointed goatgrass plants did not respond similarly to the two treatments with the same net accumulated vernalization days. The minimum vernalization requirements for plants from each jointed goatgrass population to reach the jointing and anthesis stages were estimated from frequency tables. Linear regression using PROC MIXED in SAS[8] was used to test the main and interaction effects of vernalization duration and temperature by jointed goatgrass population on GDD to the joint stage. Vernalization responses were estimated from the regression functions, and confidence intervals (α=0.05) on model intercepts and slopes were used to compare differences among populations. Actual values and confidence intervals for GDD to joint by temperature and 8-wk vernalization were used to estimate the point of maximum vernalization for all populations. Total tiller number per plant for plants vernalized 0, 4, and 8-wk was linearly regressed against GDD. Percentages for reproductive tillers produced per plant and seed germination were calculated. The minimum vernalization requirement for the mean production of reproductive tillers and germination values greater than the responses of unvernalized plants were obtained from PDIFF (α=0.05) tables in SAS.

Results and Discussion

Environmental conditions in the greenhouse were similar between repeated experiments. Plants were exposed to an average of 22 ± 2.2 GDD per d during run one, and 22 ± 2.3 GDD per d during run two. Because plants within a run were not harvested on the same day, plants were exposed to 2248-2316 GDD by harvest in the first experiment, and to 2214-2275 GDD by harvest in the second experiment. For comparison, the 30-yr GDD average per growing season at Pendleton, OR, an area where winter wheat is grown commonly and jointed goatgrass infestations are frequent, was 3084 (data not shown). Because the effects of vernalization temperatures on plant growth can be difficult to distinguish from vernalization effects on reproductive development, an alternative calculation for GDD accumulated by plants in these studies results from the sum of growth chamber and greenhouse temperatures. These values range from 2214 (unvernalized) to 2876 (8-wk vernalization at 10 C) GDD. Although the final GDD values accumulated by vernalized plants in these studies approximated the 30-yr average for field GDD, greater daily variation in field temperatures compared to growth chambers during vernalization phases complicates translation of greenhouse results to field situations.

Frequency of Plants to Joint

Greater than 80% of jointed goatgrass plants from all populations vernalized for 6-wk or longer durations reached the joint stage by the end of the experiment (Table 4.3). Populations were polymorphic for reproductive response at the 5-wk vernalization duration. The frequencies of WA-R plants to reach the joint stage declined with 5-wk vernalization at 4 and 10 C, while 90% or more of plants from WA-W, WA-S, OR-W, and OR-S reached the joint stage under similar conditions. This trend was observed also for 4-wk and shorter vernalization durations. The minimum treatment for any plant of the WA-R population to joint was 4-wk at 4 C, while unvernalized plants of the WA-W, WA-S, OR-W, and OR-S populations reached the joint stage by the end of the experiment. The responses of jointed goatgrass populations collected from spring fields (WA-S and OR-S) were similar to populations collected from traditional winter wheat/fallow fields (WA-W and OR-W).

Table 4.3. Number of jointed goatgrass plants to reach the joint stage at the conclusion of the experiment out of the number of plants grown by vernalization treatment and population.

			Jointed goatgrass				
Duration	Temp[a]	VD	WA - R	WA - W	WA - S	OR - W	OR - S
Weeks	--- C ---	Days * C	-- No. plants in joint stage / No. plants grown --				
0	0	0	0/11	11/11	11/11	10/10	11/11
2	4	56	0/8	8/10	6/10	8/9	5/9
2	7	98	0/8	5/5	9/10	9/9	9/10
2	10	140	0/10	7/9	9/10	4/8	5/10
4	4	112	5/11	10/11	9/11	11/11	8/11
4	7	196	4/11	10/10	11/11	9/11	7/11
4	10	280	4/11	10/10	11/11	11/11	10/10
5	4	140	5/10	11/11	11/11	11/11	9/9
5	7	245	7/9	9/9	10/10	11/11	10/10
5	10	350	4/10	11/11	10/11	11/11	11/11
6	4	168	10/10	10/10	9/10	10/10	9/9
6	7	294	11/11	11/11	11/11	10/10	11/11
6	10	420	9/11	11/11	9/9	11/11	9/10
6.5	4	182	8/9	9/9	7/8	9/9	8/8
6.5	7	318.5	10/10	10/10	11/11	10/10	9/9
6.5	10	455	10/11	9/11	10/10	10/10	9/9
7	4	196	9/9	9/9	9/9	9/9	7/7
7	7	343	9/10	10/10	11/11	10/10	11/11
7	10	490	8/9	9/9	10/10	10/10	10/11
8	4	224	9/9	8/8	9/9	11/11	9/9
8	7	392	10/10	11/11	11/11	11/11	9/9
8	10	560	10/10	9/9	11/11	9/9	11/11

[a] Abbreviations: Temp=temperature; VD=vernalization days; WA=Washington; OR=Oregon; R=roadside; W=winter type; S=spring type.

Frequency of Plants to Anthesis

Greater than 80% of jointed goatgrass plants from the WA-R, WA-W, WA-S, and OR-W populations vernalized for 8-wk at 4, 7, and 10 C reached the anthesis stage by the end of the experiment (Table 4.4). In contrast, fewer than 80% of OR-S plants vernalized for 8-wk at 4 and 10 C reached anthesis. The variability in reproductive responses among the populations increased among the 6, 6.5, and 7-wk vernalization duration treatments. Plants of the WA-R population consistently reached anthesis after these treatments, while plants of the WA-W, WA-S, OR-W, and OR-S populations required 7-wk vernalization at any temperature, or 6 and 6.5-wk vernalization at 7 C for most plants to reach anthesis. Fewer than 80% of all jointed goatgrass plants vernalized for 5-wk or shorter vernalization durations reached anthesis by the end of the experiment.

Table 4.4. Number of jointed goatgrass plants to reach the anthesis stage at the conclusion of the experiment out of the number of plants to reach the joint stage by vernalization treatment and population. Asterisks * mark the vernalization treatments for each population where the frequency of plants to reach anthesis was less than 80%.

			Jointed goatgrass				
Duration	Temp[a]	VD	WA - R	WA - W	WA - S	OR - W	OR - S
Weeks	--- C ---	Days * C					
0	0	0	n/a	0/11 *	0/11 *	0/10 *	0/11 *
2	4	56	n/a	0/8 *	0/6 *	0/8 *	0/5 *
2	7	98	n/a	0/5 *	0/9 *	0/9 *	0/9 *
2	10	140	n/a	0/7 *	0/9 *	0/4 *	0/5 *
4	4	112	0/5 *	1/10 *	0/9 *	0/11 *	0/8 *
4	7	196	2/4 *	0/10 *	0/11 *	0/9 *	1/7 *
4	10	280	0/4 *	0/10 *	0/11 *	0/11 *	0/10 *
5	4	140	1/5 *	0/11 *	1/11 *	0/11 *	1/9 *
5	7	245	3/7 *	1/9 *	3/10 *	6/11 *	1/10 *
5	10	350	3/4 *	0/11 *	5/10 *	1/11 *	0/11 *
6	4	168	8/10	5/10 *	5/9 *	4/10 *	5/9 *
6	7	294	11/11	9/11	7/11 *	7/10 *	10/11
6	10	420	7/9 *	0/11 *	3/9 *	2/11 *	0/9 *
6.5	4	182	8/8	6/9 *	6/7 *	7/9 *	6/8 *
6.5	7	318.5	10/10	8/10	11/11	8/10	7/9 *
6.5	10	455	10/10	5/9 *	3/10 *	5/10 *	4/9 *
7	4	196	8/9	8/9	7/9 *	5/9 *	6/7 *
7	7	343	9/9	7/10 *	11/11	7/10 *	10/11
7	10	490	8/8	7/9 *	10/10	6/10 *	6/10 *
8	4	224	9/9	8/8	9/9	9/11	7/9 *
8	7	392	10/10	10/11	11/11	9/11	8/9
8	10	560	10/10	9/9	11/11	8/9	8/11 *

[a] Abbreviations: Temp=temperature; VD=vernalization days; WA=Washington; OR=Oregon; R=roadside; W=winter type; S=spring type.

A comparison of the frequency charts for jointing and anthesis by jointed goatgrass population revealed that plants of the WA-W, WA-S, OR-W, and OR-S populations extended the period of time between the joint and anthesis stage such that plants of these populations jointed, but failed to reach the anthesis stage in the absence of vernalization. Conversely, plants of the WA-R population required a longer initial vernalization exposure to reach the joint stage, but these plants consistently reached the anthesis stage. Because jointed goatgrass has a versatile biology, estimation of the vernalization requirement in jointed goatgrass using only a single reproductive response provides a limited description of the plant's reproductive biology.

Accelerated Reproductive Development

In the absence of vernalization, WA-R jointed goatgrass plants failed to joint by the end of the experiment. Vernalization duration ($F_{1,136}$=182.11; p<0.0001), but not temperature, affected the reproductive development of these plants (Fig. 4.1). Models predicted that unvernalized WA-R plants would have jointed after 2628-2755 GDD in the greenhouse (Table 4.5). WA-R jointed goatgrass plants required at least 4-wk vernalization to joint, and each additional week of vernalization resulted in WA-R plants reaching the joint stage 230-239 GDD (approximately 10.5 d) earlier than shorter durations. In contrast, all unvernalized WA-W, WA-S, OR-W, and OR-S plants jointed by the end of the experiment (Fig. 4.1). Furthermore, plants from these populations responded similarly to increasing vernalization duration with accelerated reproductive development, and vernalization temperatures were not significantly different. Every additional week of vernalization resulted in these plant reaching the joint stage 64-114 GDD (2.8-5.1 d) earlier than shorter durations. Plants from all populations vernalized 8-wk reached the joint stage after approximately 1000 GDD in the greenhouse (Table 4.5), despite population polymorphism for vernalization responses at shorter vernalization durations.

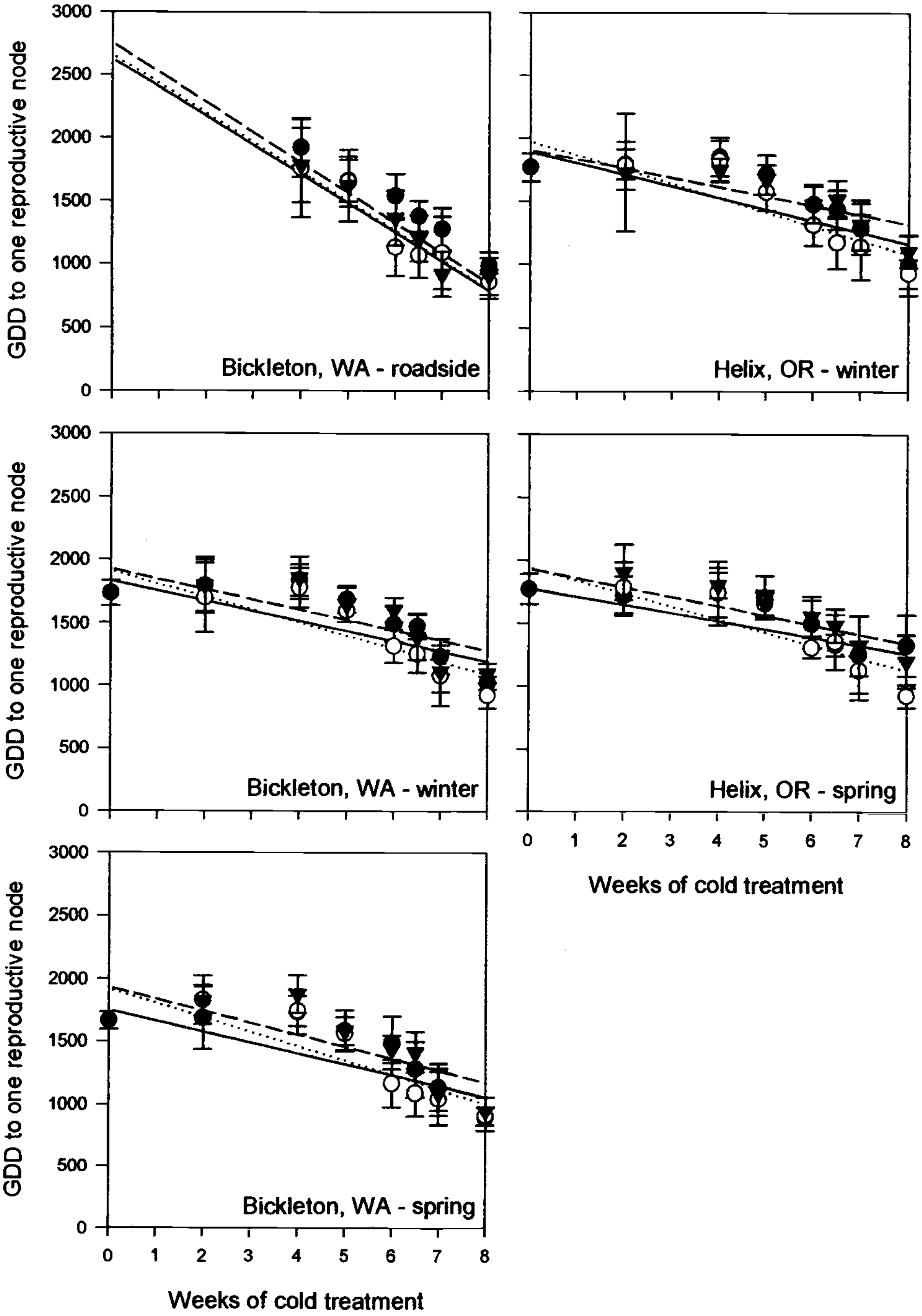

Figure 4.1. Effect of vernalization duration and temperature on the time in growing degree days (GDD) from the end of the cold treatment to the joint stage (one reproductive node) for five populations of jointed goatgrass plants. Solid circles and lines —●— represent actual and predicted values for the responses of plants vernalized at 4 C, dotted lines and open circles ·····○····· represent 7 C, and dashed lines and closed triangles --▼-- represent 10 C.

Table 4.5. Equations for the predicted GDD to joint by jointed goatgrass population and vernalization temperature as a function of vernalization duration. Confidence intervals (α=0.05) for equation intercepts and slopes are shown in parenthesis. Mean values and confidence intervals for actual GDD to joint after 8-wk vernalization are provided.

	Temperature					
	4 C		7 C		10 C	
Population	Equation	8-wk actual	Equation	8-wk actual	Equation	8-wk actual
WA - R[a]	2628(361)-230(59)*wk	984(61)	2660(377)-233(58)* wk	856(98)	2755(403)-239(61)* wk	910(185)
WA - W	1832(113)-80(22)* wk	1022(52)	1910(123)-103(22)* wk	919(102)	1924(120)-81(22)* wk	1098(78)
WA - S	1749(128)-86(25)* wk	885(97)	1919(127)-114(23)* wk	903(71)	1932(127)-95(23)* wk	947(118)
OR -W	1890(123)-91(24)* wk	997(239)	1973(128)-112(23)* wk	930(113)	1903(138)-73(25)* wk	1104(127)
OR - S	1775(122)-64(24)* wk	1328(242)	1941(121)-102(22)* wk	927(95)	1932(126)-74(23)* wk	1204(210)

[a] Abbreviations: WA=Washington; OR=Oregon; R=roadside; W=winter type; and S=spring type.

Table 4.6. Equations for the predicted tiller production by plant type and vernalization duration as a function of GDD. Confidence intervals (α=0.05) for equation intercepts are provided in parenthesis.

	Vernalization duration											
	0-wk				4-wk				8-wk			
Population	Intercept	Slope	Lower CI	Upper CI	Intercept	Slope	Lower CI	Upper CI	Intercept	Slope	Lower CI	Upper CI
WA - R	-7.35(1.43)	0.018	0.017	0.019	-4.36(0.83)	0.013	0.013	0.014	1.46(0.88)	0.004	0.004	0.005
WA - W	-8.77(1.78)	0.020	0.019	0.021	-4.97(1.06)	0.014	0.013	0.015	-1.18(1.06)	0.007	0.007	0.008
WA - S	-7.61(1.53)	0.018	0.017	0.019	-5.94(0.96)	0.015	0.014	0.016	-0.05(0.91)	0.005	0.004	0.006
OR - W	-7.06(1.42)	0.016	0.015	0.017	-4.96(0.78)	0.013	0.012	0.014	-1.64(0.79)	0.007	0.007	0.008
OR - S	-7.19(1.45)	0.016	0.015	0.017	-4.30(0.85)	0.011	0.010	0.012	-1.74(0.89)	0.007	0.007	0.008

[a] Abbreviations: WA=Washington; OR=Oregon; R=roadside; W=winter type; and S=spring type.

Tiller Number per Plant

The main effect of vernalization duration, but not temperature, affected tiller production in plants from all jointed goatgrass populations. Subsequently, tiller production numbers for jointed goatgrass plants vernalized 0, 4, and 8-wk were averaged over temperature and regressed against GDD by population in the final model. Tiller number per jointed goatgrass plants increased with increasing GDD (Fig. 4.2). The main effects of GDD and vernalization duration, and their interaction, affected the number of tillers produced by all jointed goatgrass plants. Furthermore, these effects were more pronounced than the variation in tiller production attributed to jointed goatgrass population. Jointed goatgrass plants vernalized for 8-wk produced a total of 11-16 tillers by harvest, while unvernalized plants produced 30-36 tillers by the end of the experiment. Unvernalized jointed goatgrass plants produced 16-20 tillers for every 1000 accumulated GDD, plants vernalized for 4-wk produced 11-15 tillers, and plants vernalized for 8-wk produced 4-7 tillers over a similar period (Table 4.6). Vernalized plants were older and likely had more tillers than unvernalized plants when all plants were placed initially into the greenhouse. This age difference might account for different tiller numbers during the early phases of the greenhouse experiment, and explain the interaction between GDD and vernalization duration. More importantly, differences in the rates of tiller production and subsequent final tiller numbers in response to changing vernalization duration were consistent with plants sensitive to vernalization (Chouard 1960).

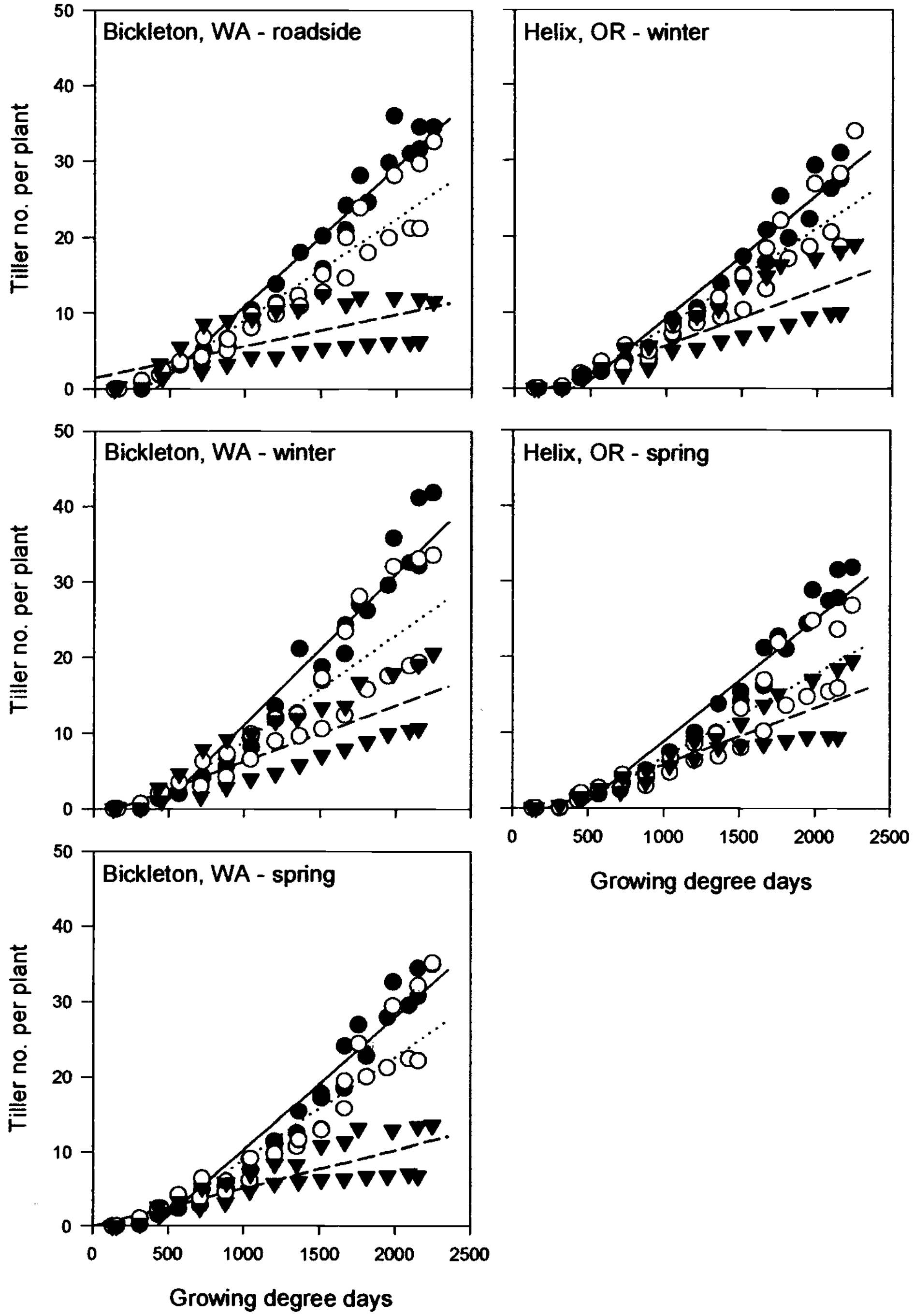

Figure 4.2. Effect of 0, 4, and 8-wk vernalization on the total number of tillers per jointed goatgrass plant as a function of time in growing degree days (GDD). Solid circles and lines —●— represent actual and predicted values for the responses of plants vernalized 0-wk, dotted lines and open circles ·····○····· represent 4-wk vernalization, and dashed lines and closed triangles --▼-- represent 8-wk vernalization. Responses were averaged over vernalization temperature.

Proportion of Reproductive Tillers

Jointed goatgrass populations differed in the minimum vernalization treatment required to produce more reproductive tillers than unvernalized plants; WA-R plants required 6-wk vernalization at 7 C, WA-W plants required 6.5-wk at 7 C, and WA-S plants required 7-wk at 4 C. Plants from both OR populations required 7-wk vernalization at 4 C (Table 4.7). These results clarify the vernalization requirements of jointed goatgrass plants within the ranges predicted by jointing and anthesis frequency charts, and they represent the minimum environmental conditions necessary to shift growth from a vegetative (accumulating tillers) to reproductive stage (accumulating spikes). Furthermore, they confirm population polymorphism for vernalization response. Although many WA-W, WA-S, OR-W, and OR-S jointed goatgrass plants vernalized for 6.5 and 7-wk reached anthesis by the end of the experiment (Table 4.4), these plants produced only one or two reproductive tillers. The variable "proportion of reproductive tillers" might be a better indicator of vernalization response because tiller numbers are distributed more normally than frequency counts based on plant number.

Seed Germination

Plants from all jointed goatgrass populations required vernalization to produce germinable seed before the end of the experiment. However, jointed goatgrass populations differed in the minimum vernalization treatment required to produce germinable seed. Plants from the WA-R population produced germinable seed when vernalized for 6-wk at 7 C, the WA-W population required 7-wk at 7 C, the WA-S required 7-wk at 4 C, the OR-W required 8-wk at 4 C, and the OR-S required 8-wk at 7 C (Table 4.8). Germination results confirm the population polymorphism distinctions for vernalization response, and identify the WA-R population as having a vernalization requirement different from plants of the WA-W, WA-S, OR-W, and OR-S populations.

Table 4.7. Percentage of reproductive tillers per jointed goatgrass plant at the conclusion of the experiment by vernalization treatment and population. Mean values and 95% confidence intervals in parenthesis are presented. An asterisk * denotes the minimum treatment for each population to produce reproductive tillers at numbers greater than 0. A condition of the asterisk is that every duration or temperature treatment greater than the minimum must increase also the percentage of reproductive tillers produced compared to the control.

			Jointed goatgrass				
Duration	Temp[a]	VD	WA-R	WA-W	WA-S	OR-W	OR-S
Weeks	--- C ---	Days * C	------------------- Reproductive tillers (%) -------------------				
0	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
2	4	56	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
2	7	98	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
2	10	140	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
4	4	112	0(0.0)	0(9.2)	0(0.0)	0(0.0)	0(0.0)
4	7	196	1(12.4)	0(0.0)	0(0.0)	0(0.0)	1(9.4)
4	10	280	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
5	4	140	0(13.0)	0(0.0)	1(11.9)	0(0.0)	1(10.4)
5	7	245	2(13.7)	1(10.2)	3(12.4)	3(10.4)	1(9.8)
5	10	350	4(13.0)	0(9.2)	1(11.9)	1(10.4)	0(9.4)
6	4	168	9(13.0)	13(9.7)	5(12.4)	8(10.9)	16(10.4)
6	7	294	47(12.4) *	12(9.2)	36(11.9)	19(10.9)	19(9.4)
6	10	420	19(12.4)	0(9.2)	7(13.1)	4(10.4)	0(9.8)
6.5	4	182	20(13.7)	4(9.7)	23(13.9)	24(11.4)	27(11.0)
6.5	7	318.5	55(13.0)	21(9.7) *	43(11.9)	40(10.9)	20(10.4)
6.5	10	455	45(12.4)	13(9.2)	8(12.4)	4(10.9)	4(10.4)
7	4	196	35(13.7)	14(9.7)	24(12.4) *	21(11.4) *	27(11.8) *
7	7	343	39(13.0)	20(9.7)	27(11.9)	41(10.9)	30(9.4)
7	10	490	44(13.7)	19(9.2)	44(12.4)	21(10.9)	19(9.4)
8	4	224	66(13.7)	36(10.2)	50(13.1)	19(10.4)	32(10.4)
8	7	392	74(13.0)	58(9.2)	56(11.9)	33(10.4)	58(10.4)
8	10	560	67(13.0)	16(9.2)	56(11.9)	25(11.4)	27(9.4)

[a] Abbreviations: Temp=temperature; VD=vernalization days; WA=Washington; OR=Oregon; R=roadside; W=winter type; and S=spring type.

Table 4.8. Percent spikelet germination by jointed goatgrass population and vernalization treatment. Mean values and 95% confidence intervals in parenthesis are presented. An asterisk * denotes the minimum treatment for each population to produce germinable seed. A condition of the asterisk is that every duration or temperature treatment greater than the minimum must produce germinable seed.

			Jointed goatgrass				
Duration	Temp[a]	VD	WA-R	WA-W	WA-S	OR-W	OR-S
Weeks	--- C ---	Days * C	-------------------	------	Germination (%)	------	-------------------
0	0	0	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
2	4	56	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
2	7	98	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
2	10	140	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
4	4	112	0(0.0)	2(10.3)	0(0.0)	0(0.0)	0(0.0)
4	7	196	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1(10.8)
4	10	280	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0(0.0)
5	4	140	9(13.7)	0(0.0)	0(11.5)	0(0.0)	8(11.9)
5	7	245	0(0.0)	0(0.0)	1(12.0)	17(21.1)	10(11.3)
5	10	350	11(13.7)	0(0.0)	3(11.5)	0(21.1)	0(10.8)
6	4	168	3(13.7)	1(10.8)	32(12.0)	12(22.1)	12(11.9)
6	7	294	57(13.0) *	14(10.3)	20(11.5)	14(22.1)	11(10.8)
6	10	420	25(13.0)	0(10.3)	11(12.7)	1(21.1)	0(11.3)
6.5	4	182	43(14.4)	1(10.8)	19(13.4)	6(23.3)	8(12.6)
6.5	7	318.5	52(13.7)	28(10.8)	15(11.5)	34(22.1)	10(11.9)
6.5	10	455	54(13.0)	25(10.3)	8(12.0)	9(22.1)	19(11.9)
7	4	196	35(14.4)	6(10.8)	30(12.0) *	8(23.3)	17(13.5)
7	7	343	48(13.7)	27(10.8) *	32(11.5)	35(22.1)	27(10.8)
7	10	490	28(14.4)	22(10.3)	37(12.0)	28(22.1)	20(10.8)
8	4	224	59(14.4)	30(11.4)	28(12.7)	79(21.1) *	16(11.9)
8	7	392	69(13.7)	47(10.3)	43(11.5)	58(21.1)	29(11.9) *
8	10	560	67(13.7)	21(10.3)	52(11.5)	38(23.3)	28(10.8)

[a] Abbreviations: Temp=temperature; VD=vernalization days; WA=Washington; OR=Oregon; R=roadside; W=winter type; and S=spring type.

Conclusions

Vernalization influences the growth of winter cereals by allowing plants to escape cold injury (Flood and Halloran 1986) and accelerating reproductive development before summer drought (Baskin and Baskin 1974). Our results confirm the quantitative vernalization requirement of jointed goatgrass reported by Donald (1984) and assert polymorphism among jointed goatgrass populations for vernalization requirements. Jointed goatgrass plants of WA-W, WA-S, OR-W, and OR-S populations required fewer vernalization days to reach the joint stage than 'Madsen' (Allan et al. 1989) winter wheat (Fandrich 2005). However, jointed goatgrass populations were polymorphic for this reproductive response, and plants of the WA-R population required a longer vernalization period than Madsen plants to reach the joint stage. While a 6-wk vernalization duration represents the minimum vernalization requirement for reproductive development among a jointed goatgrass population, Madsen and Madsen related hybrids, the risk of gene transfer might be greater when the onset of reproductive development is most similar - after 7-wk vernalization.

A spring crop rotation might effectively reduce, but not eliminate, jointed goatgrass infestations as part of an integrated weed-management plan. In the jointed goatgrass populations tested, there has not been selection for a spring-type growth habit. However, if spring temperatures were cool, minimum conditions for vernalization might be satisfied, and jointed goatgrass plants could complete their life cycle. Additionally, the production of vernalization insensitive plants from a cross between spring wheat and jointed goatgrass plants documents an increased potential for the transfer of spring type alleles into jointed goatgrass populations (Fandrich 2005). Because spring wheat and jointed goatgrass have been observed nicking during anthesis in Oregon fields (Morrison et al. 2002), spring cropped fields should be scouted for jointed goatgrass and wheat by jointed hybrid plants, and these plants removed before seed production and dissemination.

A confounding factor in the modeling of jointed goatgrass vernalization requirements was revealed by the longer period between jointing and anthesis observed in WA-W, WA-S, OR-W, and OR-S jointed goatgrass populations compared to the WA-R population and Madsen winter wheat. Selection in Madsen winter wheat for rapid reproductive development once the vernalization requirement has been met insures that the crop matures synchronously and predictably in the field. The specific vernalization conditions, limited temperature variability, and more detailed observations in the greenhouse vernalization study revealed reproductive differences among jointed goatgrass populations not previously observed in field vernalization studies (Fandrich 2005). The persistence of jointed goatgrass populations would be favored by an extended and/or non-synchronous reproductive period. Jointed goatgrass seed produced under a wide range of environmental conditions might have different germination requirements, thus insuring population survival over time.

Acknowledgements

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Sources of Materials

[1] Osmocote 14-14-14. The Scotts Company, 14111 Scottslawn Road, Marysville, OH 43041.

[2] BB44 Steel Blue Blotter. Hoffman Manufacturing Inc., International Agri-Supply, 353 29th Avenue SW, Albany, OR 97321.

[3] Cont156C Transparent Acrylic Container. Hoffman Manufacturing Inc., International Agri-Supply, 353 29th Avenue SW, Albany, OR 97321.

[4] RLC7 Stubby Cell. Stuewe & Sons, Inc., 2290 SE Kiger Island Drive, Corvallis, Oregon 97333-9425.

[5] Sunshine Mix #1/LC 1, 15831 N.E. 8th Street, Suite 100, Bellevue, WA 98008.

[6] Peters Professional 20-20-20. The Scotts Company, 14111 Scottslawn Road, Marysville, OH 43041.

[7] Fulex Nicotine Fumigator. EPA No. 1327-41. Fuller System, Inc., 226 Washington Street, Woburn, MA 01801.

[8] SAS, Version 8.2. SAS Institute Inc., Cary, NC, USA.

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CHAPTER 5

Temperature Effects on Jointed Goatgrass (*Aegilops cylindrica*) Seed Germination

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A better understanding of the persistence of jointed goatgrass seed in soil and its dormancy will lead to the development of more effective weed-management strategies. Three populations of jointed goatgrass were collected from winter wheat fields in Oregon, and grown together with the winter wheat variety 'Madsen' in nurseries at Moro and Pendleton, OR. Germination responses of jointed goatgrass and wheat seed were recorded over 14 d incubation at 5/5, 15/10, 15/15, 25/15, 25/25, and 30/20 C day/night temperatures and a 12-h photoperiod. Because jointed goatgrass spikelets often contain two seed, primary and secondary seed germination values were recorded. Secondary seed germination was defined as 3-mm radicle protrusion, and primary seed germination was defined as 5-mm emergence of the second coleoptile. Jointed goatgrass secondary seed germinated when exposed to all temperature regimes. Jointed goatgrass secondary seed germination occurred 3 d earlier in regimes involving a 15 C temperature compared to germination at 5/5, 25/25, and 30/20 C. Final germination values for jointed goatgrass secondary seed were greatest when seed were incubated at 25/15 C. Wheat seed germinated at all temperature regimes, although the onset of germination occurred 1 to 1.5 d later at 5/5 C compared to other temperature regimes. Jointed goatgrass primary seed germinated only at 15/10, 15/15, and 25/15 C, and maximum germination occurred at 25/15 C. Dormancy in jointed goatgrass might prevent germination of seed within freshly shattered spikelets until autumn when temperatures are low and moisture is available. Because final germination percentages in jointed goatgrass primary and secondary seed were less than 100%, additional research on factors regulating dormancy is needed.

Nomenclature: Jointed goatgrass, *Aegilops cylindrica* Host, AEGCY; wheat, *Triticum aestivum* L., 'Madsen'.

Keywords: Alternating temperatures, thermal dormancy.

Jointed goatgrass (*Aegilops cylindrica* Host) is a winter annual weed and relative of domesticated bread wheat (*Triticum aestivum* L.). It was introduced into the United States in the late 1800s (Johnston and Heyne 1960), and spread rapidly over 3 million ha

(Anonymous 2002). Reduced yields, decreased land values, increased dockage, and increased control measures cost winter wheat producers nationwide $145 million annually (Ogg 1993). Because jointed goatgrass and wheat germination, growth, and development are similar (Dotray and Young 1988; Fenster and Wicks 1976; Johnston and Parker 1929), strategies for control of jointed goatgrass have been limited to cultural practices, crop rotation, tillage, and the use of herbicide resistant wheat. Integrated management practices specific to several winter wheat production regions have been recommended for jointed goatgrass control (Evans et al. 1999; Pester et al. 1999; Young et al. 2002). Integrated weed-management strategies for control of many other weed species have been improved through contributions of seed dormancy models that simulate germination in response to agronomic, environmental, and genetic influences (Buhler et al. 1997; Dyer 1995; Foley 2001; Taylorson 1987).

Although jointed goatgrass has been the subject of many studies, a full characterization of its dormancy has not been reported. Gleichsner (1987) reported that jointed goatgrass was under the control of thermal dormancy, i.e., more seed germinated at low rather than high temperatures, but the experiment was not repeated, and alternating temperature regimes were not tested. Morrow et al. (1982) reported that seed of freshly harvested jointed goatgrass spikelets germinated at 10, 15, and 20 C, but not at higher temperatures. There has been no published data to specify seed germination within spikelets, despite occurrences of heteroblasty in related species (Datta et al. 1970; Wurzburger & Koller 1976). Current literature describes jointed goatgrass germination on a per spikelet basis, even though most spikelets have more than one seed (Donald and Zimdahl 1987).

Temperature is a major environmental factor that affects the persistence of dormancy in temperate grasses and influences germination after seed imbibe water (Simpson 1990). Mature seed may germinate to 100% at all temperatures (non-dormant), between 0 and 100% at low but not at high temperatures (thermally dormant), or not at any temperature (dormant). As dormant and partially dormant seed after-ripen, germination occurs over a broader range of temperatures such that narrow, specific requirements for germination are lost (Vegis 1964). Furthermore, lack of germination only at unfavorable temperatures represents a minimum or low level of dormancy (Taylorson 1987), and a requirement for a diurnal change from a lower to a higher temperature represents a greater level of dormancy. Thompson and Grime (1983) investigated the effect of fluctuating temperatures on the germination of 112 herbaceous species. Forty-six of the species examined were found to have their germination stimulated by temperature fluctuations.

Parameters commonly used to describe the germination time course and compare dormancy levels in different populations or treatments include germination onset, rate, and theoretical maximum germination (Roche et al. 1997; Burke et al. 2003). Predicted germination responses are usually modeled using a logistic function:

$$\mathrm{Y} = M(1 + \exp[-K(t - L)])^{-1} \qquad [5.1]$$

where Y is the cumulative percent germination at time t, M is the asymptote or theoretical maximum germination for Y, L is the time scale constant, or lag to onset of germination, and K is the rate of increase (Roche et al. 1997). Typically, a logistic function is run on each treatment combination, and treatment effects compared using standard errors or confidence intervals on the three parameter estimates. When the temperature regime is optimum for jointed goatgrass germination, primary and secondary seed will germinate earlier, have faster germination rates, and have higher maximum cumulative germination percentages compared to other temperature regimes. A significant increase in at least one of these parameters indicates that germinability was altered by the temperature treatment and is a biologically meaningful result.

The objective of this study was to characterize dormancy in freshly harvested jointed goatgrass seed. Because jointed goatgrass is a winter annual species, it was hypothesized that freshly harvested seed would germinate best at low temperatures.

Materials and Methods

Mature spikelets of naturalized jointed goatgrass populations were collected in 2001 from winter wheat fields in northcentral and eastern Oregon. Spikes were clipped from the plants when the culms appeared dry at the base of the plant, and when the physiological black layer was present in exhumed and laterally cut seed. Spikes were broken apart, spikelets were hand-cleaned to remove culms and debris, and samples were stored dry until use.

Three populations of jointed goatgrass and the winter wheat variety 'Madsen' were grown during the 2001-02 season in field nurseries at the Columbia Basin Agricultural Research Center in Pendleton, Oregon, and the Sherman County Experiment Station in Moro, Oregon. Winter wheat was included in the study as a non-dormant standard; post-harvest seed dormancy only lasts a few days in most common wheat varieties (Larson et al. 1936; Chang 1943; Ching and Foote 1961). Nursery sites were selected from areas without a history of jointed goatgrass infestation. Jointed goatgrass spikelets and winter wheat seed (n=45) were sown 3 cm deep into 2-m rows spaced 60 cm apart. Thirty g of slow-release, granular fertilizer[1] was evenly scattered down the furrow. Sites were hand-weeded as necessary, and no other maintenance was required. At maturity, intact spikes from jointed goatgrass populations were harvested by row and stored at -30 C within 24 h. A storage temperature of -20 C was shown to delay seed dormancy losses after maturity in wheat (Nyachiro et al. 2002) and wild oat (*Avena fatua*) (Foley 1994). Jointed goatgrass samples were cleaned as described previously and returned to cold storage in less than 30 min.

Tetrazolium viability tests were conducted on jointed goatgrass seed. Two replicates of 100 spikelets were soaked in water for 1 h at room temperature (22 ± 2 C). The glumes, lemmas, and paleas were removed, and seed were sorted by floret position. Seed were soaked in a 0.5% aqueous 2,3,5-triphenyl tetrazolium chloride[2] solution overnight at room temperature in the dark. Seed were evaluated using guidelines described in the Association of Official Seed Analysts Tetrazolium Testing Handbook No. 29 (Peters 2000). The total number of seed by floret position and number of seed testing positive for viability were recorded.

Germination Description and Definition

The jointed goatgrass inflorescence is composed of spikelets arranged alternately along the main axis of the spike. Each spikelet may produce two to five florets (Hitchcock 1950; Johnston and Parker 1929; McGregor 1987), and seed are produced usually in the lower two positioned florets (primary and secondary). In contrast to wheat, jointed goatgrass seed do not freely thresh from the glumes (Heyne 1950; Johnston and Parker 1929). Primary seed remain attached to the lower positioned glume, while secondary seed are attached to the upper positioned glume. Identification of lower and upper positioned seed based on glume position during germination experiments can be time consuming and disruptive to water uptake. Preliminary research has shown that the seed positioned in the secondary floret usually germinates first (Fandrich, personal observation), and can be defined by radicle emergence. (Morrow et al., 1982, reported that the largest seed within spikelets consistently germinated first. We have observed that the larger seed grows in the second or third [if present] positioned floret, and the smaller seed grows in the primary positioned floret.) The primary positioned seed germinates later, but it is not possible to distinguish the radicle of the primary positioned seed among established secondary seed roots. Germination of the primary positioned seed can be confirmed only with the emergence of its coleoptile. Because the secondary positioned seed has already germinated, and subsequently a coleoptile has emerged from the spikelet, germination of the primary seed can be confirmed only with the emergence of the *second* coleoptile.

Germination tests were conducted in growth chambers set to 5/5, 15/10, 15/15, 25/15, 25/25, and 30/20 C and a 12-h photoperiod. Intact spikelets and seed from each stored population and nursery location were placed on two 10.2-by-10.2 cm germination blotters[3] wetted with 25 ml deionized water in similarly sized, clear, covered acrylic germination boxes[4]. Eight germination boxes (two population by nursery location combinations) were placed together on trays on separate shelves in a growth chamber and rotated within the chamber every 2 d to minimize shelf effects. Observations were made every 2 d. Germination of the secondary positioned seed was recorded when approximately 3-mm of the radicle emerged from the spikelet. Germination of the primary positioned seed was recorded when 5-mm of the second coleoptile emerged from the spikelet. Wheat seed germination was defined as 3 mm radicle emergence. Additional water was added as visually determined. All germination tests were conducted using four sub-samples of 16 non-terminal and 4 terminal or 21 non-terminal and 4 terminal jointed goatgrass spikelets from each stored population; 20 or 25 randomly selected wheat seed were used in each subsample. The tests were run for 14 d and were repeated.

Percent germination values were calculated by dividing the cumulative number of germinated spikelets or seed with emerged radicles or spikelets with 2 coleoptiles by the adjusted total number of spikelets or seed in the box. Positive results from tetrazolium assays were used to adjust for viable seed numbers (Table 5.1). Visual analysis of graphed data confirmed there were no differences between repeated experiments. Logistic regression models (Eq. 5.1) common for analysis of percent germination data were fit to the combined data. Significantly different results were distinguished from one another using sum of squares tests. Parameter estimates were compared using confidence intervals (α=0.05) around the predicted values. Jointed goatgrass germination analyses were run separately for germination defined by 1) emergence of the radicle and 2) emergence of the second coleoptile.

Table 5.1. Average number of seed per 100 jointed goatgrass spikelets by floret position, positive results of tetrazolium chloride tests, and predicted final germination values. Tertiary floret data are not shown.

	Primary floret						Secondary floret					
			Positive		Predicted germination[b]				Positive		Predicted germination	
	--- No.[a] ---		------------ % ------------				--- No. ---		------------ % ------------			
Population	M[a]	P[a]	M	P	M	P	M	P	M	P	M	P
Rufus, OR	87	83	94	87	81	72	67	70	99	94	66	65
Athena, OR	93	84	92	90	85	75	73	72	100	95	73	68
Helix, OR	91	90	90	90	81	81	74	69	94	96	69	66
LSD $_{(0.05)}$[c]	NS	NS	NS	NS			NS	NS	NS	NS		

[a] Abbreviations: No., number of seeds; M, Moro, OR; and P, Pendleton, OR nurseries.

[b] Calculated from the product of seed number and percent tetrazolium chloride positive.

[c] Denotes values required for significance at α=0.05 among jointed goatgrass populations within a nursery location.

Results and Discussion

Jointed Goatgrass Secondary Seed and Wheat Seed Germination

Jointed goatgrass secondary seed germinated when exposed to all temperature regimes ranging from 5/5 to 30/20 C (Fig. 5.1). Germination onset (*L*) (Equation 5.1) and maximum percent (*M*) were influenced by incubation temperature, but rate (*K*) was not affected by temperature. Jointed goatgrass secondary seed germinated within 6 d at regimes involving a 15 C temperature compared to 10 d at 5/5, 25/25, and 30/20 C (Table

5.2). Final germination values for jointed goatgrass secondary seed were greatest when seed were incubated at 25/15 C. Ninety percent of secondary seed germinated in a population collected from Athena, OR. Wheat seed germinated to nearly 100% at all regimes, although the onset of germination occurred 1 to 1.5 d later at 5/5 C compared to the other temperatures. Wheat germination rates (*K*) were unaffected by temperature.

Jointed goatgrass secondary seed final germination values varied by population at temperature regimes above 25/15 C. Seed of the Athena, OR, population germinated to 78 and 73%, when grown at Moro and Pendleton, respectively, and were incubated at 25/25 C. In contrast, the Rufus, OR, population, germinated to 29 and 65% under the same conditions. Germination values of the Helix, OR population were within the range of values from the Athena and Rufus populations.

Jointed goatgrass Primary Seed Germination

Primary seed germinated only under regimes involving a 15 C temperature (Table 3). Final germination values for jointed goatgrass primary seed were greatest when seed were incubated at 25/15 C. The lag period for primary seed germination was approximately 10 d, and final germination values were less than 25%. Models did not converge on these data, and germination rates were not estimated. Because final germination values were less than values predicted by seed number and viability tests (Table 5.1), dormancy in the primary seed contributes significantly to jointed goatgrass population dormancy. Tertiary positioned seed did not germinate; however, less than 1% of spikelets produce three seed (Donald and Zimdahl 1987). The current study did not address dormancy cycling in jointed goatgrass seed.

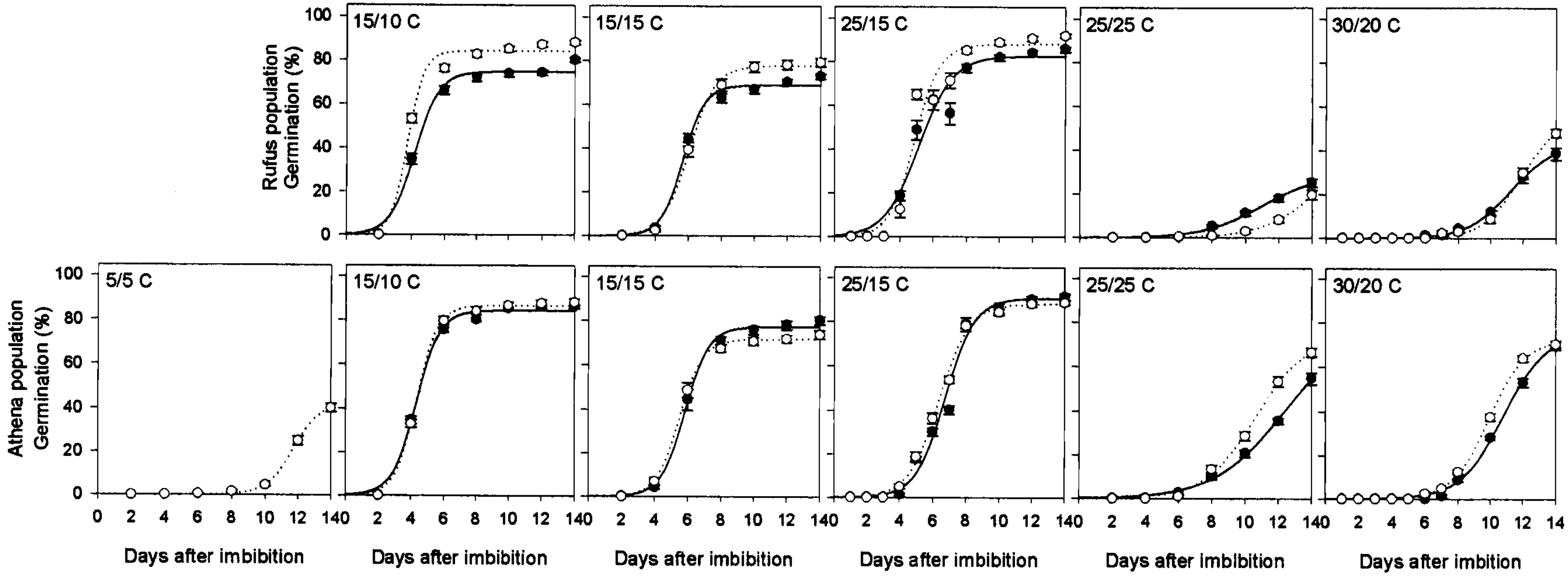

Figure 5.1. Germination defined as radicle emergence grouped by population and incubation temperature. 1 = Rufus, OR population; 2 = Athena, OR population; 3 = Helix, OR population; 4 = wheat 'Madsen' variety; a = 5/5 C; b = 15/10 C; c = 15/15 C; d = 25/15 C; e = 25/25 C; f = 30/20 C. Lines represent predicted values; symbols represent means and contain standard error bars. Solid lines and closed circles are data from populations grown at the Moro, OR nursery, while dotted lines and open circles are data from populations grown at the Pendleton, OR nursery.

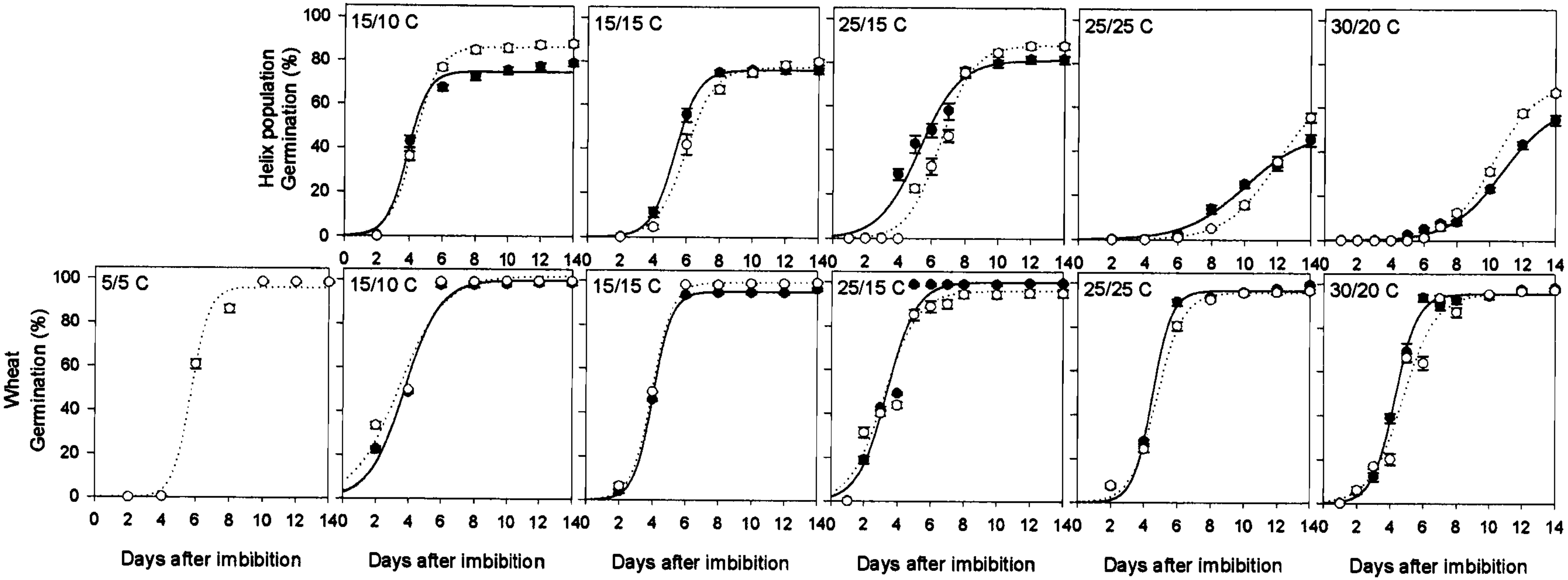

Figure 5.1 (Continued). Germination defined as radicle emergence grouped by population and incubation temperature. 1 = Rufus, OR population; 2 = Athena, OR population; 3 = Helix, OR population; 4 = wheat 'Madsen' variety; a = 5/5 C; b = 15/10 C; c = 15/15 C; d = 25/15 C; e = 25/25 C; f = 30/20 C. Lines represent predicted values; symbols represent means and contain standard error bars. Solid lines and closed circles are data from populations grown at the Moro, OR nursery, while dotted lines and open circles are data from populations grown at the Pendleton, OR nursery.

Table 5.2. Parameter estimates and confidence intervals ($\alpha=0.05$) for the predicted secondary seed germination of three jointed goatgrass populations and winter wheat grown at two locations in 2001-02. Germination was defined as 3 mm of radicle protusion.

			Estimate ± confidence interval ($\alpha=0.05$)					
Population	Loc.[a]	Parameter[b]	5/5 C[c]	15/10 C	15/15 C	25/15 C	25/25 C	30/20 C
Rufus, OR	M	M		74 ± 3.0	68 ± 3.1	82 ± 3.4	29 ± 18.8	43 ± 15.1
	M	K		1 ± 0.4	1 ± 0.6	0 ± 0.2	0 ± 0.5	0 ± 0.4
	M	L		4 ± 0.2	5 ± 0.2	5 ± 0.2	10 ± 3.1	11 ± 1.3
Rufus, OR	P	M		84 ± 2.8	77 ± 3.6	87 ± 3.2	65 ± 714.3	55 ± 18.6
	P	K		1 ± 1.1	1 ± 0.4	1 ± 0.3	0 ± 1.2	0 ± 0.5
	P	L		3 ± 0.2	6 ± 0.2	4 ± 0.2	15 ± 31.9	11 ± 1.1
Athena, OR	M	M		84 ± 3.4	77 ± 3.6	90 ± 3.8	78 ± 50.3	75 ± 13.2
	M	K		1 ± 0.4	1 ± 0.5	1 ± 0.2	0 ± 0.2	0 ± 0.2
	M	L		4 ± 0.2	5 ± 0.2	6 ± 0.2	12 ± 3.1	10 ± 0.7
Athena, OR	P	M	42 ± 10.0	86 ± 3.0	71 ± 3.2	88 ± 3.2	73 ± 13.0	72 ± 7.3
	P	K	1 ± 0.8	1 ± 0.5	1 ± 0.4	1 ± 0.2	0 ± 0.2	0 ± 0.2
	P	L	11 ± 0.6	4 ± 0.2	5 ± 0.2	6 ± 0.2	10 ± 0.8	9 ± 0.4
Helix, OR	M	M		74 ± 3.0	75 ± 3.3	81 ± 3.9	48 ± 14.3	61 ± 15.7
	M	K		1 ± 0.8	1 ± 0.4	0 ± 0.2	0 ± 0.3	0 ± 0.2
	M	L		3 ± 0.2	5 ± 0.2	5 ± 0.3	10 ± 1.5	10 ± 1.2
Helix, OR	P	M		85 ± 3.0	77 ± 3.5	87 ± 3.8	70 ± 28.4	71 ± 9.6
	P	K		1 ± 0.4	1 ± 0.3	1 ± 0.2	0 ± 0.3	0 ± 0.2
	P	L		4 ± 0.2	5 ± 0.2	6 ± 0.2	11 ± 1.6	10 ± 0.6
Wheat	M	M		99 ± 2.2	95 ± 2.0	100 ± 2.0	96 ± 2.1	95 ± 2.0
	M	K		0 ± 0.1	1 ± 0.5	1 ± 0.1	1 ± 0.3	1 ± 0.2
	M	L		3 ± 0.1	4 ± 0.1	3 ± 0.1	4 ± 0.1	4 ± 0.1
Wheat	P	M	95 ± 2.8	101 ± 3.1	99 ± 2.6	96 ± 2.7	95 ± 2.9	95 ± 3.0
	P	K	1 ± 0.7	0 ± 0.1	1 ± 0.5	0 ± 0.2	1 ± 0.2	1 ± 0.1
	P	L	5 ± 0.1	3 ± 0.2	4 ± 0.1	3 ± 0.2	4 ± 0.2	4 ± 0.2

[a] Location 'M' grown at Moro, OR; location 'P' grown at Pendleton, OR.

[b] M=asymptotic germination percentage; K=germination rate; L=days to germination.

[c] Day/night incubation temperature and 12-h photoperiod.

Germination of freshly harvested jointed goatgrass seed promoted by low temperatures was similar to Gleichsner (1987) and Morrow et al. (1982). Thermal dormancy prevents germination during the summer, even if rain wets the soil, because soil temperatures are above those required for germination. High summer temperatures are required for dormancy loss in the seed of most grasses behaving as winter annuals, especially in regions with a temperate climate (Baskin and Baskin 1998a). Additionally, research presented herein clarified that jointed goatgrass seed germinated better with alternating temperature regimes compared to constant regimes. High temperatures, widely fluctuating temperatures, fire, drying, freeze/thaw cycles and passage through animal digestive tracts are known to erode the surfaces of seed coats and permit germination of dormant seed (Baskin et al. 2000). Although final germination values were low for primary positioned seed at all temperatures, germination is still biologically significant. In situations where the soil remains cool through the spring, there may be a low and yet significant portion of seed that can germinate, emerge, and cause economic losses for growers.

Our research confirmed polymorphism for seed germination among jointed goatgrass populations, as was shown for other species (Evans and Cabin 1995; Frost and Cavers 1975; Naylor and Abdalla 1982; Paterson et al. 1976). Because the original seed populations were collected within a limited geography and from fields with similar crop histories, it is hypothesized that germination discrepancies at high temperatures among populations do not reflect selection for different ecotypes. Rather, germination variability might be part of a general purpose genotype strategy to promote germination and colonization in a wide range of environments (Silvertown and Charlesworth 2001). Jointed goatgrass is a polyploid species, and may have up to four different alleles for the genes that control dormancy and germination. Donald and Zimdahl (1987) reported also different germination patters for two populations of jointed goatgrass buried over 5 yr.

The success of a weed might depend in part on a delay in its germination until conditions are suitable for plant growth (Baker 1974). Genetic control and environmental influences on the developing and shattered seed contributed to the variation in jointed goatgrass dormancy and germinability. Given the broad geographic distribution of jointed goatgrass, there are likely many populations with differing germination requirements. Jointed goatgrass seed dormancy models may be improved further by studying populations gathered from environments across the western United States. Because germination values were less than 100%, factors other than temperature are regulating seed dormancy in freshly harvested jointed goatgrass.

Table 5.3. Germination means and confidence intervals (α=0.05) for three jointed goatgrass populations grown at two locations in 2001-02 at 10, 12, and 14 d after imbibition. Germination was defined as 5-mm emergence of the second coleoptile. Second coleoptiles did not emerge from spikelets incubated at 5/5, 25/25, and 30/20 C.

		Primary seed germination (%)								
		15/10 C[a]			15/15 C			25/15 C		
Population	Loc.[b]	d 10	d 12	d 14	d 10	d 12	d 14	d 10	d 12	d 14
Rufus, OR	M	1 ± 1.1	1 ± 1.1	2 ± 2.4	0 ± 0.0	1 ± 1.1	1 ± 1.1	3 ± 2.2	4 ± 2.9	6 ± 3.4
Rufus, OR	P	2 ± 1.7	4 ± 3.1	6 ± 4.3	1 ± 1.4	5 ± 4.4	8 ± 4.9	7 ± 6.6	9 ± 6.2	11 ± 8.4
Athena, OR	M	2 ± 2.5	3 ± 3.0	3 ± 3.0	3 ± 3.5	3 ± 4.6	4 ± 4.5	1 ± 1.4	4 ± 5.8	11 ± 6.4
Athena, OR	P	5 ± 3.4	7 ± 4.7	7 ± 4.9	1 ± 1.1	3 ± 3.5	4 ± 3.1	11 ± 6.0	15 ± 5.0	22 ± 8.3
Helix, OR	M	3 ± 3.0	3 ± 3.0	3 ± 3.0	1 ± 1.1	1 ± 1.1	2 ± 2.4	0 ± 0.0	2 ± 2.1	5 ± 3.8
Helix, OR	P	11 ± 3.9	12 ± 4.3	13 ± 4.8	1 ± 1.5	10 ± 7.2	13 ± 7.9	4 ± 2.9	8 ± 5.8	13 ± 8.0

[a] Day/night incubation temperature and 12-h photoperiod.

[b] Location ‘M’ grown at Moro, OR; location ‘P’ grown at Pendleton, OR.

Sources of Materials

[1] Osmocote 14-14-14. The Scotts Company, 14111 Scottslawn Road, Marysville, OH 43041.

[2] Fisher Scientific Company, 1458 N. Lamon Avenue, Chicago, IL 60651.

[3] BB44 Steel Blue Blotter. Hoffman Manufacturing Inc., International Agri-Supply, 353 29th Avenue SW, Albany, OR 97321.

[4] Cont156C Transparent Acrylic Container. Hoffman Manufacturing Inc., International Agri-Supply, 353 29th Avenue SW, Albany, OR 97321.

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CHAPTER 6

Factors Affecting Germination of Jointed Goatgrass (*Aegilops cylindrica*) Seed

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Specific knowledge on the dormancy, germination, and emergence patterns of weed species aids the development of integrated management strategies. The after-ripening period for jointed goatgrass seed was quantified, and the effects of germination conditions and spikelet structures on jointed goatgrass seed germination were studied. As the duration of after-ripening increased, jointed goatgrass seed germinated earlier, at faster rates, and to greater final percentages compared to non-after-ripened seed. Both primary and secondary positioned seed within jointed goatgrass spikelets were non-dormant after 16 weeks after-ripening at 22 ± 2 C. Germination of dormant seed depended on incubation temperature and dark/light conditions. Sixty-seven percent of spikelets produced a radicle when exposed to low temperatures in the dark, and light reduced germination by 7%. Although the effects of light and dark conditions on secondary positioned seed germination were statistically significant, the results may be a function of biological variability. However, the effect of light and warm temperatures promoted primary seed germination, or the emergence of the second coleoptile from the spikelet, and is more likely part of this seed's germination requirement. Coleoptile emergence was dependent on planting depth for three jointed goatgrass populations, winter wheat, and spring wheat. Under optimum conditions in the greenhouse, no planting depth selectively allowed wheat germination and emergence while preventing jointed goatgrass germination and emergence. Glume removal increased jointed goatgrass secondary positioned seed final germination percent to 96%, increased the germination rate, and decreased the number of days required to reach 50% germination to 6 d. Glume removal promoted also germination of the primary seed within jointed goatgrass spikelets. Unmodified spikelets failed to produce two coleoptiles. Glume removal resulted in 80% of the spikelets having two coleoptiles, but did not alleviate dormancy completely in jointed goatgrass seed.

Nomenclature: Jointed goatgrass, *Aegilops cylindrica* Host, AEGCY; wheat, *Triticum aestivum* L., TRZAW.

Keywords: after-ripening, dormancy, light, spikelet.

Jointed goatgrass (*Aegilops cylindrica* Host) is a winter annual weed in winter wheat (*Triticum aestivum* L.) production regions across the central and western regions of the USA. Winter wheat producers lose an estimated $145 million annually to jointed goatgrass through reduced yields, decreased land values, increased dockage, and increased control measures (Ogg 1993). Jointed goatgrass control is difficult because of its common ancestry with wheat, both species have the D genome (Zemetra et al. 1998), and their growth and development are similar (Donald and Ogg 1991). Jointed goatgrass is adapted to the central and western regions of the USA where lack of rainfall restricts production choices mostly to a winter wheat-fallow rotation or continuous winter wheat (Donald and Ogg 1991). The persistence of jointed goatgrass seed in soil for up to three years (Donald and Zimdahl 1987) limits the success of crop-fallow and annual crop rotations as control measures. An understanding of jointed goatgrass seed dormancy and germination requirements may aid the effectiveness of cultural practices, crop rotation, tillage, and the use of herbicide-resistant wheat as control measures.

Dormancy is an important characteristic for propagation of weed species that reproduce by seed (Baker 1974). Seed from jointed goatgrass are produced and shed in early to mid-summer, and are exposed immediately to hot soil surface temperatures and limited soil moisture. Survival of a germinated seed through these conditions is unlikely. The presence of dormancy delays germination until autumn when optimum temperatures and adequate moisture for germination and growth are available. These same hot and dry conditions over time may alleviate seed dormancy through a process described as after-ripening (AR) - the interaction between seed and environment over time that leads to dormancy loss (Simpson 1990). The events that lead to dormancy loss during AR are not well understood. Permeability of seed coat membranes may be affected with the net effect of increased rates of water absorption (Chippindale 1933; Conover and Geiger 1984) or gas exchange (Simpson 1990).

Quantification of jointed goatgrass seed AR requirements provides a description of time and environment necessary to relieve completely dormancy in jointed goatgrass seed. However, current literature fails to accurately describe the effect of AR on jointed goatgrass seed. Gleichsner reported that jointed goatgrass seed gained the ability to respond to a wider range of temperatures over a 0.5 to 12 month period (1987), but additional results were not published. Morrow et al. (1982) observed that more 1 yr old seed germinated at temperatures ranging from 10 to 35 C than did freshly harvested seed, but shorter AR time periods were not tested. Preliminary results showed that jointed goatgrass seed germination was improved with 3 weeks AR at 22 ± 2 C in dark, dry conditions (Fandrich and Mallory-Smith 2003). Further research on the effect of AR on jointed goatgrass seed germination is warranted. Control measures designed to remove germinated seedlings will be most effective when the majority of seed in the seed bank are non-dormant.

Exposure to light breaks dormancy in many weed species, but there are species in which light has no effect or even inhibits germination. Baskin and Baskin (1998a) summarized that among 54 grass species, germination of 28 was promoted by light, 13 were unaffected by light or dark conditions, and 13 were inhibited by light. Milberg et al. (1996) tested 44 species, mostly agricultural weeds, and found that germination improved in 24 species after a five second exposure to light. In the remaining 20 species, there was no effect or an inconsistent response. Because light has been shown to be a significant germination factor for many weed species (Bewley and Black 1994), cultivation at night has been to used successfully reduce the germination of weeds in newly established crops (Hartmann and Nezadal 1990; Klaffke 1998).

The effect of light on germination of jointed goatgrass seed is unclear. Cleary and Peeper (1980) reported in field studies that more jointed goatgrass spikes were produced on plants that established on the soil surface than plants that emerged from 5 or 16 cm. Jointed goatgrass infestations were more frequent also in areas where producers have adopted conservation tillage (Schweitzer et al. 1988), possibly because more spikelets are left on the soil surface compared to conventional tillage. However, jointed goatgrass seed remain inside the glumes (Heyne 1950; Johnston and Parker 1929), and the receptivity of the seed to light is not known, nor has selection for light sensitivity been tested. Alternatively, jointed goatgrass seed germination may be insensitive to light and dark conditions. Jointed goatgrass emerged best when spikelets were sown 0 to 3 cm deep in greenhouse studies (Morrow et al. 1982), and deeper sowings reduced the number of emerged seedlings. These results led Baskin and Baskin (1998b) to surmise that jointed goatgrass seed germinate equally well in light and dark.

Jointed goatgrass seed germination may be a function of AR and germination environments, and also under the influence of spikelet structures surrounding the seed. The potential for spikelet structure influence on jointed goatgrass seed germination exists because of its flowering biology. The inflorescence in jointed goatgrass is composed of spikelets arranged compactly and alternately along the main axis of the spike (Hitchcock 1950; Johnston and Parker 1929; McGregor 1987). The spike axis disarticulates below each set of glumes, and the dispersal unit of jointed goatgrass is a spikelet. The lemma and the palea adhere tightly to jointed goatgrass seed, and the florets remain attached to the glumes (Heyne 1950; Johnston and Parker 1929). The lemma and palea in wild oat (*Avena fatua* L.) contain germination inhibitors (Chen et al. 1982), and contribute to gas exchange limitations to and from the caryopsis (Hay and Cumming 1959). The physical influence of the glumes, lemma, and palea on jointed goatgrass seed germination is not known. Separation of seed within an imbibed jointed goatgrass spikelet appeared to stimulate germination of both seed within one day (Fandrich, personal observation).

The objectives of this study were to 1) quantify the AR period, 2) examine the effects of light and dark environments through germination experiments in the laboratory and burial depth experiments in the greenhouse, and 3) test the effect of spikelet structure removal on germination.

Materials and Methods

After-ripening Duration

Mature spikelets of a jointed goatgrass population were collected in 2001 from a winter wheat field near Helix, Oregon. Spikes were clipped from the plants after the culms dried, and were placed in paper bags. In the laboratory, spikes were broken apart, spikelets were cleaned by hand, and sub-samples were stored dry at 22 ± 2 C or at -30 C within 24 h after harvest. Jointed goatgrass plants were grown during the 2001-02 field season from 45 spikelets sown 3 cm deep in a 2 m row in a field nursery at the Columbia Basin Agricultural Research Center in Pendleton, OR. Slow-release, granular fertilizer[1] was applied in the furrow at planting. The nursery was hand-weeded as necessary. At maturity, spikes from jointed goatgrass plants were harvested as previously described, and stored at -30 C to maintain levels of seed dormancy. A storage temperature of -20 C delayed seed dormancy losses in wheat (Nyachiro et al. 2002) and wild oat (*Avena fatua*) (Foley 1994). Spikelets were cleaned and returned to cold storage in less than 30 minutes.

Spikelet samples were removed periodically from -30 C storage, and after-ripened for different time periods under dry, dark conditions at ambient room temperature. Minimum and maximum room temperatures were recorded daily for 30 d at three intervals during the after-ripening period. AR treatments were defined by time: 0 (control), 3, 5, 12, 16, 20, 25, and 30 wks. Samples were removed from storage so that all AR treatments concluded on the same day. Twenty-five spikelets were placed into 10.2 by 10.2 cm germination boxes containing moistened 'steel blue' blotter paper[2]. Boxes were covered and placed inside germination chambers set to 25/15 C day/night temperatures and 12 hr photoperiod. Observations were made daily. Jointed goatgrass spikelets often contain two seed (Donald and Zimdahl 1987), and the larger seed, located in the second floret, usually germinates first (Fandrich and Mallory-Smith 2005; Morrow et al. 1982).When approximately a 3 mm radicle had emerged from the spikelet, germination for the secondary positioned seed was recorded. When the second coleoptile emerged from the spikelet, germination of the primary positioned seed was recorded. Blotter paper moisture levels were kept constant for the duration of the germination test. The test was conducted for 21 days, contained four replicates for each after-ripening treatment, and was repeated in space using an additional growth chamber.

Germination as a percent of total spikelets was plotted against days after imbibition for each AR treatment. Analysis of graphed data confirmed that data by treatment were similar between repeated tests. A non-linear regression model often used in germination studies (Burke et al. 2003; Shafii and Barney 2001) was fit to the data for each AR treatment using SAS[3]. Significantly different regression parameters on the predicted germination time course were distinguished from one another using sum of squares tests (α=0.05). Analyses were run separately for germination defined as 1) radicle emergence and 2) emergence of the second coleoptile.

Light and Dark Effects

Laboratory test

Jointed goatgrass spikelets were harvested by hand in 2001 from a winter wheat field located near Athena, OR at the completion of the 2000-01 winter wheat field season. Spikelets were returned to the laboratory within 24 h, the sample divided, and spikelet sub-samples stored at 22 ± 2 C to AR for 1 yr or at -30 C to maintain dormancy.

After-ripened and dormant spikelet samples were placed in germination boxes as previously described. In addition, boxes designated for a 'dark' treatment were wrapped immediately with two layers of heavy duty aluminum foil[4]. Boxes were placed in growth chambers set to 15/15 C (cool) and 30/20 C (warm) day/night temperatures and 12 hr photoperiod. After 7 d, boxes and aluminum foil were removed, and the number of germinated spikelets per box counted. Because spikelets often contain two seed, germination values were recorded for spikelets with 3 mm radicle emergence and for spikelets with 2 coleoptiles.

The experiment was repeated with seed of the same population produced in field nurseries at the Sherman County Experiment Station in Moro, OR, and at the Columbia Basin Agricultural Research Center in Pendleton, OR, respectively. Planting procedures, nursery maintenance, and harvest procedures were as described previously. Climate data were collected from weather stations nearest the collection and nursery sites. Spikelet germination data were subjected to analysis of variance (ANOVA) for a factorial experiment arranged in a completely randomized design using SAS. Preliminary analysis showed the effect of dormancy was four times greater than that of its interaction with photoperiod or incubation temperature. Data were analyzed separately for germination of dormant and non-dormant spikelets. Main effects were photoperiod and incubation temperature. Data from repeated experiments had similar magnitudes and variances, and were combined. The effect of photoperiod on primary and secondary seed germination within a dormancy group and incubation temperature was evaluated using the pdiff t-test option in SAS.

Greenhouse test

Jointed goatgrass spikelets were harvested by hand in 2001 from mature plants in winter wheat fields located near Bickleton, WA, Helix, OR, and Athena, OR. Spikelets were returned to the laboratory, cleaned as described previously, and stored dry at ambient laboratory temperature.

The effect of planting depth on jointed goatgrass and wheat seed germination and coleoptile emergence was investigated in the greenhouse. Groups of 8 or 12 intact after-ripened jointed goatgrass spikelets from each population, winter wheat cultivar 'Madsen' seed, and spring wheat cultivar 'Penewawa' seed were planted at depths of 0, 0.6, 2.5, 5.1, 7.6 and 10.2 cm from the soil surface into 3.8 L pots filled with commercial potting mix[5]. Pots were placed in a greenhouse maintained at 18/15 C day/night temperatures and 12 hr photoperiod, and watered to keep the soil surface moist. Coleoptile emergence and germination were quantified 14 d after planting. Coleoptiles were considered emerged if shoots appeared at the soil surface. Plant heights and dried biomass were measured by clipping the coleoptiles at the soil surface. Spikelets and seed were exhumed to quantify germination. Germination was defined as 3 mm radicle protrusion from the seed or spikelet.

The study was arranged as a completely randomized design with four replicates for each population or species and planting depth. The experiment was repeated. Percentage data were analyzed by ANOVA and main effect means separated by Fisher's protected LSD (α=0.05). Data were pooled when preliminary analysis revealed no difference between repeated experiments.

Spikelet Structures

Jointed goatgrass spikelets used in this study were from the same seed source as used in the 'After-ripening Duration' experiment.

Spikelets were removed from cold storage, and were soaked in deionized water to soften structures for easy removal. Spikelets were soaked for up to 3.5 hr, and dry, unmodified spikelets served as a control. Germination boxes were prepared and filled as previously described with spikelets that were 1) unmodified and dry; 2) unmodified and soaked, 3) lacked a rachis segment and dry; 4) lacked a rachis segment and soaked; 5) lacked glumes and dry; and 6) lacked glumes and soaked. Seed from the "no glumes" treatments were sorted by floret position and placed accordingly into separate germination boxes. A sample of 15 week AR spikelets were included as a dormancy loss standard. AR conditions were previously described.

Boxes were placed inside germination chambers set to 25/15 C day/night temperature and 12 hr photoperiod. The number of germinated spikelets was recorded daily as previously described except for seed in the "no glumes" treatment. Germination in this treatment was defined only as 3 mm radicle emergence. Blotter paper moisture levels were maintained over the duration of the test. Tests were conducted for 21 days. Percent germination by primary and secondary seed was plotted against incubation time for each structure modification and soaking treatment. Analysis of graphed data confirmed that data were similar for dry and soaked spikelets, and data were combined. Non-linear regression analysis was performed on the data as described in the 'After-ripening Duration' experiment.

Results and Discussion

After-ripening Duration

Mean daily temperature for the AR treatments was 22 ± 2 C. As the duration of after-ripening increased, jointed goatgrass secondary seed germinated earlier, at faster rates, and to greater final percentages compared to secondary seed in the dormant sample. Dormant secondary seed germinated to 85%, and an AR period of three weeks improved germination to 96% (Fig. 6.1). Additional AR did not improve final germination values. Germination rates increased, and germination lags decreased, such that there were no further changes in these parameters beyond 12 weeks AR (Table 6.1). Primary seed within dormant spikelets germinated to 20% after 21 d incubation (Fig. 6.2). Three weeks AR resulted in 49% germination, and final germination values increased through 12 weeks AR. Germination rates of primary seed did not increase beyond 12 weeks. However, 16 weeks AR shortened the time required to reach 50% germination.

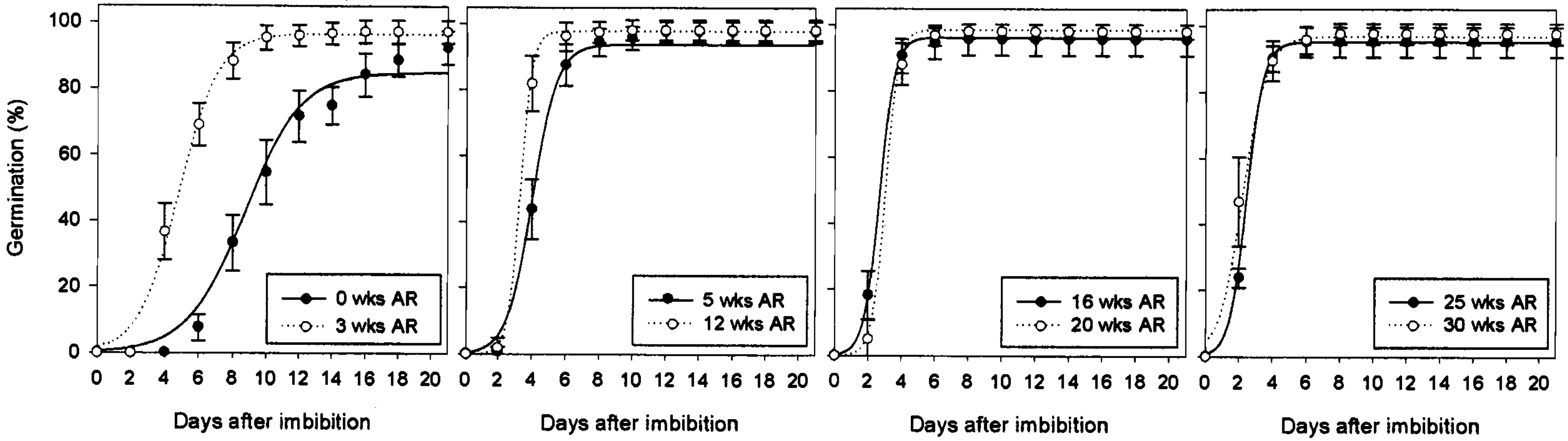

Figure 6.1. Cumulative germination of the second positioned seed in a jointed goatgrass spikelet, defined as radicle emergence, grouped by after-ripening treatment. Lines represent predicted values; symbols represent means and contain confidence intervals (α=0.05).

Table 6.1. Parameter estimates and confidence intervals (α=0.05) for predicted secondary and primary seed germination of a jointed goatgrass population after-ripened at 22 ± 2 C for eight durations. Germination of the secondary seed was defined as 3 mm of radicle protusion, and germination of the primary seed was defined as emergence of the second coleoptile.

		0 wks	3 wks	5 wks	12 wks	16 wks	20 wks	25 wks	30 wks
		Germination estimate ± confidence interval (α=0.05)							
	Parameter[a]	%							
Secondary[b]	M	85 ± 2.3	96 ± 2.1	94 ± 1.6	98 ± 1.8	96 ± 1.5	99 ± 1.5	95 ± 1.8	97 ± 1.5
	K	0.6 ± 0.1	0.9 ± 0.1	1.4 ± 0.3	2.8 ± 1.3	2.2 ± 0.4	2.6 ± 0.5	2.0 ± 0.6	1.4 ± 0.3
	L	8.7 ± 0.3	4.8 ± 0.2	4.1 ± 0.1	3.4 ± 0.3	2.8 ± 0.2	3.1 ± 0.2	2.6 ± 0.2	2.3 ± 0.1
Primary[b]	M	30 ± 70.1	49 ± 13.6	51 ± 4.0	74 ± 3.0	62 ± 2.3	69 ± 2.3	77 ± 2.7	65 ± 2.3
	K	0.4 ± 0.5	0.3 ± 0.1	0.5 ± 0.2	1.2 ± 0.4	1.8 ± 1.0	2.1 ± 1.4	2.0 ± 1.4	1.7 ± 0.7
	L	19.8 ± 14.0	13.6 ± 2.6	10.1 ± 0.7	6.8 ± 0.3	5.6 ± 0.3	5.7 ± 0.3	5.7 ± 0.3	5.6 ± 0.3

[a] M=asymptotic germination percentage; K=germination rate; L=days to 50% germination.

[b] Seed floret position within the spikelet.

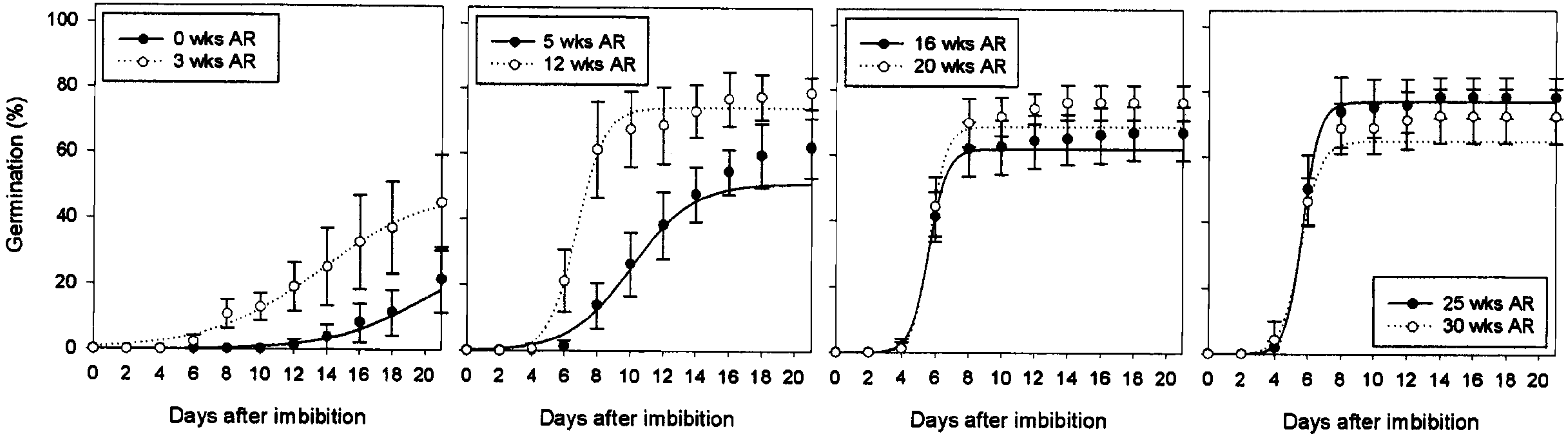

Figure 6.2. Cumulative germination of the primary positioned seed in a jointed goatgrass spikelet, defined as emergence of the second coleoptile, grouped by after-ripening treatment. Lines represent predicted values; symbols represent means and contain confidence intervals (α=0.05).

Because approximately 2 d passed between the emergence of the radicle and the first coleoptile (Fandrich, personal observation), germination lag parameters separated by less than 2 d were not different. When adjusted for the germination criteria, the germination lags for primary seed AR for 16 weeks or longer were similar to the lags in the same time period for secondary seed. Subsequently, both seed within jointed goatgrass spikelets were non-dormant after 16 weeks AR.

The short dormancy periods for secondary and primary seed in jointed goatgrass suggest that nearly all of the seed would germinate in the fall or spring after shattering if moisture were available. Our results predict that jointed goatgrass should exhibit a transient seed bank, with seed turnover of less than one year (Grime 1981). However, germinable jointed goatgrass seed remain in soil for 3-5 yr (Lish et al. 1988; Donald and Zimdahl 1987). Jointed goatgrass seed persist in the soil via dormancy cycling (Donald 1991), and we hypothesize that the persistent soil seed bank can be attributed to induction of secondary dormancy in the primary positioned seed. Only seed with the capacity for primary dormancy can be induced into secondary dormancy (Symons et al. 1986, 1987). Despite a short dormancy period, three or more years of rotation outside of winter annual crops may be necessary to reduce populations of jointed goatgrass.

Light and Dark Effects

Temperature and moisture conditions for jointed goatgrass grown at the collection site and nursery sites were similar (data not shown). Germination of dormant spikelets depended on incubation temperature and dark/light conditions. Sixty-seven percent of spikelets produced a radicle when exposed to low temperatures in the dark, and light at low temperatures reduced germination by 7% (Fig. 6.3a). In contrast, less than 1% of spikelets germinated when exposed to warm temperatures, and light *increased* germination by 7%. None of the incubated dormant spikelets produced a second coleoptile. The influences of temperature and dark/light conditions on germination defined as radicle emergence in non-dormant spikelets was similar; light affected germination by 6% (Fig. 6.3b). The relationship between light and incubation temperature was similar also for germination of the primary positioned seed in non-dormant spikelets; however, the magnitude of the effect increased. Light increased germination of seed incubated at warm temperatures by 18% (Fig. 6.4). Because germination values were less than 80% predicted by the occurrence of two seed in the spikelet (Donald and Zimdahl 1987), the primary positioned seed in AR spikelets maintained a dormancy status that was not completely relieved by germination conditions. The combined effects of exposure to low temperature and light may reduce germination in natural environments because a greater risk of freeze damage exists at the soil surface, whereas warm temperatures and light are evidence of good growing conditions and promote germination.

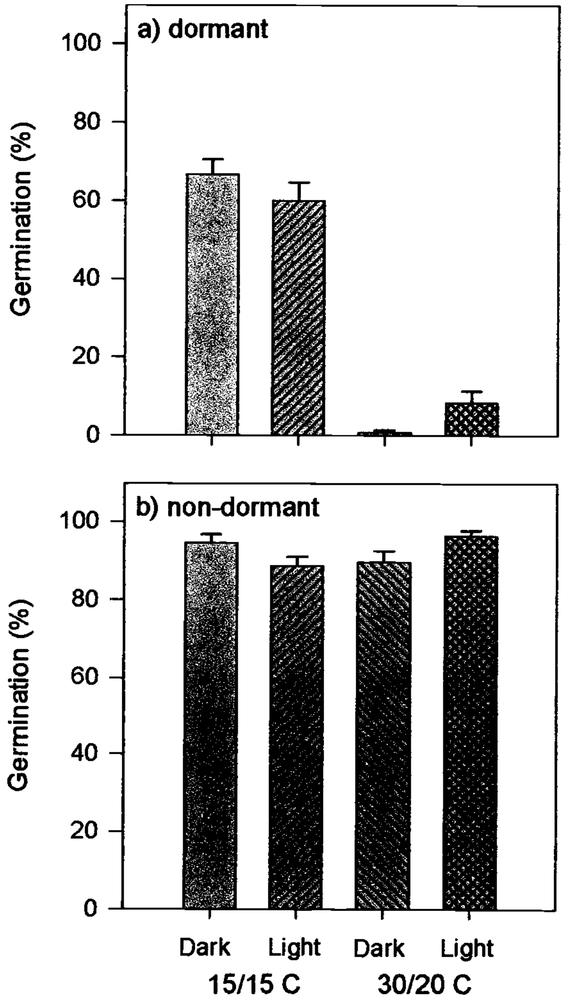

Figure 6.3. Mean percent germination, defined as radicle emergence, and confidence intervals (α=0.05) for the second positioned seed in a) dormant and b) non-dormant jointed goatgrass spikelets grouped by temperature and dark/light conditions.

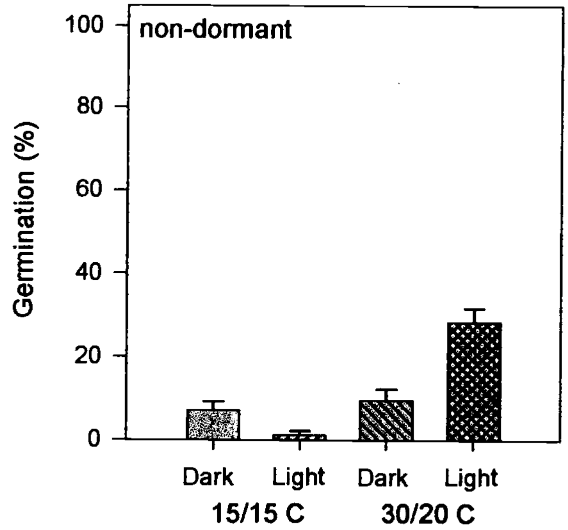

Figure 6.4. Mean percent germination, defined as emergence of the second coleoptile, and confidence intervals (α=0.05) for the primary positioned seed in non-dormant jointed goatgrass spikelets grouped by temperature and dark/light conditions.

Germination of jointed goatgrass has been shown previously to be insensitive to light and dark conditions (Baskin and Baskin 1998b). Although the effects of light and dark conditions on germination of the secondary seed in these studies were significant, the results may be a function of biological variability rather than seed dormancy. The effect was comparatively small, and it was observed similarly in dormant and non-dormant seed. However, the effect of light and warm temperatures on primary seed germination was greater, and is more likely part of this seed's germination requirement. Jointed goatgrass spikelets often contain two seed (Donald and Zimdahl 1987), and the smaller of the two is located in the primary positioned floret. In circumstances where light promotes germination, it has been associated with small, rather than large, seed masses (Koller et al. 1964; Milberg et al. 2000; Schutz et al. 2002). Data on jointed goatgrass germination responses support the hypothesis that light acts as a depth sensing cue to avoid fatal germination of small seed buried too deep in the soil.

Coleoptile emergence was dependent on planting depth for the three jointed goatgrass populations, winter wheat, and spring wheat. Surface and shallow plantings up to 5.1 cm resulted in similar emergence percentages for coleoptiles of jointed goatgrass, winter wheat, and spring wheat (Table 6.2). Winter and spring wheat coleoptiles emerged to greater final percentages than jointed goatgrass when seed and spikelets were sown 7.6 cm. However, less than 50% of winter and spring wheat coleoptiles emerged from 7.6 cm, despite good germination (Table 6.3). Under optimum conditions in the greenhouse, no planting depth selectively allowed wheat germination and emergence while preventing jointed goatgrass germination and emergence.

Table 6.2. Percent emergence of three jointed goatgrass populations, winter wheat, and spring wheat planted in the greenhouse at six soil depths.

	Emergence percentage[a]				
	Jointed goatgrass			Winter wheat	Spring wheat
Depth	Bickleton, WA	Athena, OR	Helix, OR		
cm	%				
0	88 AB a	97 A a	99 A a	88 AB a	73 B a
0.6	90 A a	98 A a	98 A a	94 A a	84 A a
2.5	85 AB ab	93 AB a	96 A a	92 AB a	79 B a
5.1	71 B b	77 AB b	86 AB a	90 A a	78 AB a
7.6	25 C c	26 BC c	17 C b	42 AB b	47 A b
10.2	2 A d	4 A d	2 A b	15 A c	10 A c

[a] Letters represent differences at $\alpha=0.05$ according to confidence intervals on the mean responses of eight replicates. Uppercase letters indicate differences among jointed goatgrass populations and wheat types at the same planting depth. Lowercase letters indicate differences among planting depths for the same jointed goatgrass population or wheat type.

Table 6.3. Percent germination of three jointed goatgrass populations, winter wheat, and spring wheat planted in the greenhouse at six soil depths.

	Germination percentage[a]				
	Jointed goatgrass			Winter wheat	Spring wheat
Depth	Bickleton, WA	Athena, OR	Helix, OR		
cm	%				
0	88 A a	97 A a	99 A a	88 A a	73 B a
0.6	91 A a	98 A a	99 A a	94 A a	86 A a
2.5	87 AB a	94 AB a	98 A a	95 AB a	82 B a
5.1	83 A a	96 A a	92 A a	92 A a	84 A a
7.6	82 B a	90 AB a	87 AB a	97 A a	78 B a
10.2	94 AB a	92 AB a	99 A a	97 A a	82 B a

[a] Letters represent differences at $\alpha=0.05$ according to confidence intervals on the mean responses of eight replicates. Uppercase letters indicate differences among jointed goatgrass populations and wheat types at the same planting depth. Lowercase letters indicate differences among planting depths for the same jointed goatgrass population or wheat type.

Because jointed goatgrass and wheat are genetically related, seed size between the species may be similar and account for similar emergence from various planting depths. There are no published reports of measuring directly seed size in jointed goatgrass, but Heyne (1950) reported that 1.7 seed were produced per spikelet and they account for 48% of the joint weight. The average mass of 100 spikelets from 43 populations in our laboratory was 4.1 g (data not shown). Based on these data, the thousand kernel weight of jointed goatgrass seed was calculated as 19.8 g. Wheat seed size varies with market class and variety, and ranges of 26.0 to 36.0 g thousand kernel weight are common. Direct measurements of jointed goatgrass seed mass by floret position are necessary to test the seed size hypothesis. Most often, the larger seed in the jointed goatgrass germinates first and competes with wheat for resources. The seed weight reported by Heyne (1950) includes the average of both seed, and a value of 19.8 g as thousand kernel weight for jointed goatgrass may underestimate the thousand kernel weight for the large seed in a jointed goatgrass spikelet.

In these experiments, jointed goatgrass coleoptiles emerged well from all shallow soil depths. Similar germination values for spikelets on the soil surface and buried 10.2 cm confirm that the first coleoptile produced by jointed goatgrass germinates equally well in dark and light. Because only one coleoptile emerged from spikelets after 14 d, the effect of burial depth on germination of the primary positioned seed, or the second coleoptile, could not be tested.

Spikelet Structures

Germination of the secondary seed from dormant samples was consistent with data reported previously. A radicle emerged from approximately 80% of the spikelets by the end of the germination test, and these seed required 9 d to reach 50% germination (Fig. 5a). Removal of the rachis segment did not affect germination (Table 6.4). Glume removal increased the percent of spikelets with radicles to 96%, increased the germination rate, and decreased the number of days required to reach 50% germination to 6 d (Fig. 5c). However, glume removal did not alleviate dormancy completely in jointed goatgrass secondary seed. Secondary seed in the after-ripened sample germinated also to 96%, and the germination rates were similar, but 50% germination in the AR treatment occurred by day three (Fig. 5e). Unmodified spikelets in dormant samples failed to produce two coleoptiles. However, glume removal resulted in 80% of the spikelets producing two coleoptiles (Fig. 5d). Dormancy in primary seed was not lost completely by glume removal. After-ripened primary seed germinated faster and reached 50% germination 8 d earlier (Fig. 5e) compared to germination of primary seed in the 'no glumes' treatment. In addition, data confirm that the secondary positioned seed in the spikelet germinated before the primary seed (Table 6.4). Observations for germination on a per spikelet basis and for germination of the secondary positioned seed were similar.

Seed removal from spikelet structures improved germination also in many related *Aegilops* species. A biochemical inhibitor identified in *Aegilops kotschy* (Wurzburger and Leshem 1969) reduced germination by approximately 80% (Wurzburger et al. 1974). Absence of the hulls in *Ae. ovata* differentially promoted germination based on seed position within *Ae. ovata* spikes and spikelets (Datta et al. 1970). *Ae. ovata* seed differed in sensitivity to a monoepoxylignanolide compound identified in the hulls (Lavie et al. 1974). Vanillic acid, present in the structures surrounding *Ae. tauschii*, reduced germination of non-dormant *Ae. tauschii* seed by approximately 75% (Gatford et al. 2002). An influence of the spikelet structures attributed to a biochemical inhibitor reduced germination of primary positioned seed in *Ae. triuncialis* by 20 to 50% (Dyer 2004). Jointed goatgrass primary positioned seed germination stimulated by the removal of spikelet structures is within the ranges reported for other *Aegilops* species. Multiple reports that identify biochemical inhibitors in the glumes of other *Aegilops* species suggest a similar mechanism of dormancy may exist in jointed goatgrass seed.

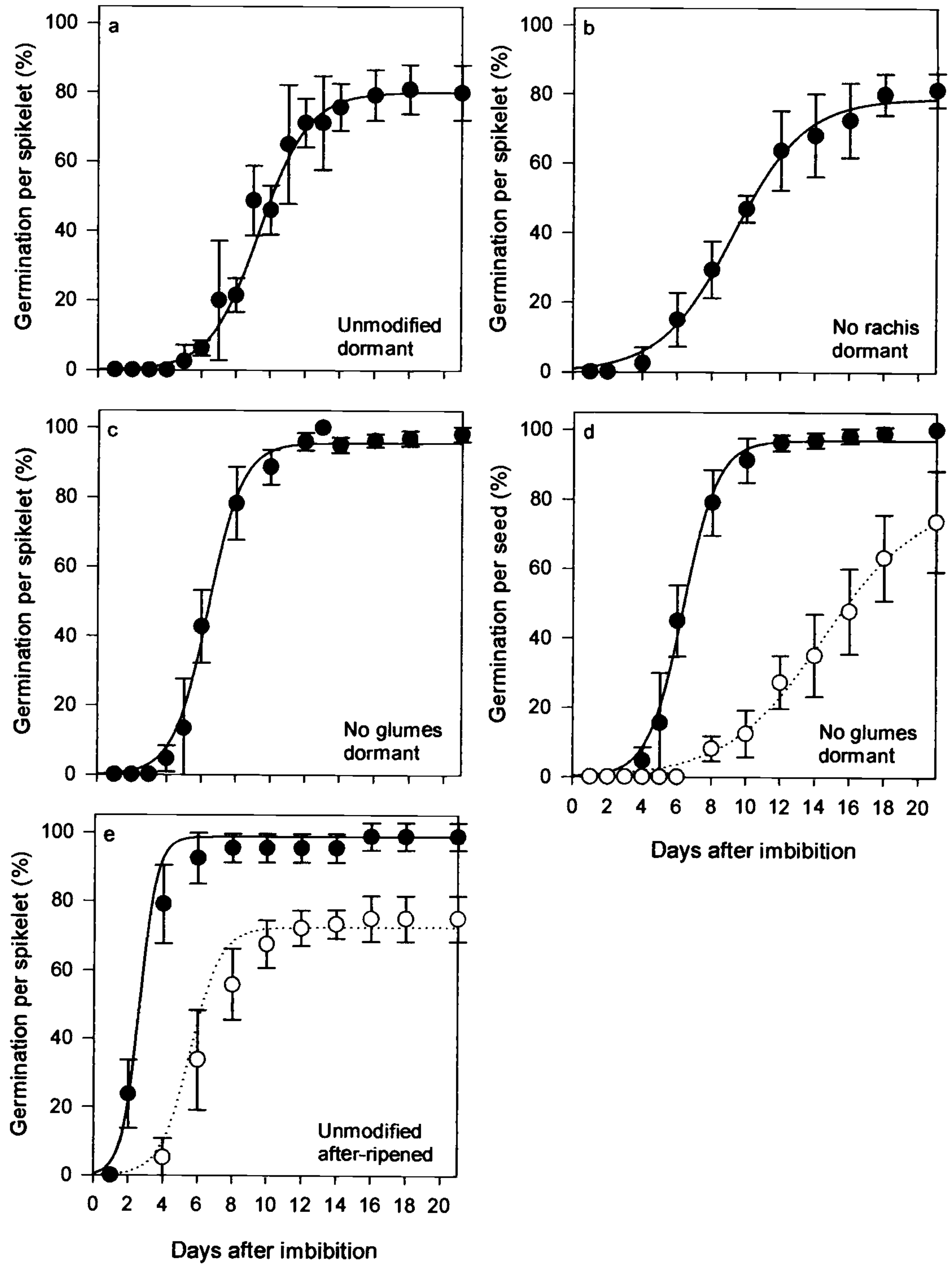

Figure 6.5. Cumulative germination on a per spikelet and per seed basis grouped by spikelet structure removal treatment. Lines represent predicted values; symbols represent means and contain confidence intervals (α=0.05). Solid lines and closed circles represent secondary seed germination, and dotted lines and open circles represent primary seed germination.

Table 6.4. Parameter estimates and confidence intervals (α=0.05) for predicted jointed goatgrass secondary and primary seed germination influenced by spikelet structures.

		Dormant[a]	No rachis[a]	No glumes[a]	NG prim.[bc]	NG sec.[bc]	AR 15 weeks[ac]
		Germination estimate ± confidence interval (α=0.05)					
	Parameter[d]	%					
Radicle	M	80 ± 2.9	79 ± 4.1	96 ± 2.2	n/a	97 ± 2.2	96 ± 1.9
	K	0.7 ± 0.1	0.5 ± 0.1	1.0 ± 0.2	n/a	1.0 ± 0.1	1.4 ± 0.2
	L	9.3 ± 0.3	9.2 ± 0.5	6.4 ± 0.2	n/a	6.3 ± 0.2	2.9 ± 0.2
Two coleoptiles	M	0	0	n/a	80 ± 11.7	n/a	73 ± 3.5
	K	0	0	n/a	0.4 ± 0.1	n/a	0.8 ± 0.2
	L	0	0	n/a	14.5 ± 1.2	n/a	6.4 ± 0.4

[a] Germination of the secondary seed was defined as 3 mm of radicle protusion, and germination of the primary seed was defined as emergence of the second coleoptile.

[b] Germination was defined as 3 mm radicle emergence.

[c] Abbreviations: NG=no glumes, AR=after-ripened.

[d] M=asymptotic germination percentage; K=germination rate; L=days to 50% germination.

Jointed goatgrass seed after-ripens and loses dormancy at warm temperatures after approximately 4 months. Because spikelets mature and shatter in July, all secondary and most primary positioned seed are capable of germinating with rain in September and October. Dormancy cycling was not studied in our experiments, but Donald (1991) showed that cycling was present in jointed goatgrass seed. Secondary seed within jointed goatgrass spikelets germinated well in light and dark conditions in the laboratory and greenhouse. Tillage may reduce emergence of seedlings derived from primary positioned seed because germination of these seed was promoted by light and warm temperatures. The influence of spikelet structures reduced germination of the primary seed. Germination tests on seed removed from spikelet structures confirm that the secondary positioned seed within jointed goatgrass spikelets germinated before the primary positioned seed. Repeated wet/dry cycles, alternating temperatures, warm temperatures, and biotic interactions may weaken the influences of the spikelet structures on the primary seed during the after-ripening period to promote germination in autumn.

Sources of Materials

[1] Osmocote 14-14-14. The Scotts Company, 14111 Scottslawn Road, Marysville, OH 43041.

[2] BB44 Steel Blue Blotter. Hoffman Manufacturing Inc., International Agri-Supply, 353 29th Avenue SW, Albany, OR 97321.

[3] SAS, Version 8.2. SAS Institute Inc., Cary, NC, USA.

[4] Reynolds wrap heavy duty aluminum foil. Reynolds Consumer Products. Richmond, VA, 23261.

[5] Sunshine Mix #1/LC 1, 15831 N.E. 8th Street, Suite 100, Bellevue, WA 98008.

Acknowledgements

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CHAPTER 7

Jointed Goatgrass Seed Germination and Production Varies by Spikelet Position on the Spike

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Integrated management techniques for several USA winter wheat production regions have been proposed for jointed goatgrass control. These strategies may be improved by a greater understanding of genetic and environmental influences on seed development and germination. Six jointed goatgrass populations were studied to test the effect of inflorescence position on seed dormancy and seed production. Jointed goatgrass populations were collected from Oregon and Washington fields and grown together in common garden nurseries. Unbroken spikes for each population were hand-collected at maturity, and stored at -30 C to slow dormancy loss or stored at 22 ± 2 C to after-ripen. Germination tests were conducted on dormant and after-ripened samples in growth chambers set to 25/15 C and 12 hr photoperiod. Spikelet position on the spike affected germination of the secondary positioned seed within jointed goatgrass spikelets in dormant samples. Seed from spikelet positions 1 to 6 germinated earlier, faster, and to greater final percentages than seed from positions 7, 8, and 9. In contrast, spikelet position did not affect germination in after-ripened samples. Spikelet position affected also primary seed germination in dormant samples. In a Bickleton, WA dormant sample, more seed germinated from positions 2, 3, and 4 than seed from positions 1 and 5 to 7. Seed were produced in all three florets within spikelets collected from the original sites. However, more seed were produced in tertiary florets of jointed goatgrass spikelets from Bickleton, WA compared to the population from The Dalles, OR. Greater seed production in tertiary florets of the Washington population was observed also when Oregon and Washington jointed goatgrass populations were grown in common garden experiments. Efforts to model the life history of jointed goatgrass and predict germination should be adjusted to account for population diversity and seed inflorescence position.

Nomenclature: jointed goatgrass, *Aegilops cylindrica* Host, AEGCY.
Keywords: diversity, dormancy.

Jointed goatgrass (*Aegilops cylindrica* Host) is a weedy relative of bread wheat (*Triticum aestivum* L.) that was introduced into the United States in the late 1800s (Johnston and Heyne 1960). It is found today throughout the continental United States, but concentrated mostly over 3 million ha of winter wheat production areas in the Pacific Northwest and Central Great Plains (Anonymous 2002). Jointed goatgrass is found also in pastures, along roadsides, fencerows, field access roads, and other disturbed areas. Winter wheat producers lose an estimated $145 million annually to jointed goatgrass via reduced yields, increased dockage, increased control measures, and decreased land values (Ogg 1993). Selective control of jointed goatgrass is difficult because of its common ancestry with wheat, and jointed goatgrass and wheat germination, growth, and development are similar (Dotray and Young 1988; Fenster and Wicks 1976; Johnston and Parker 1929). Integrated management techniques specific to several USA winter wheat production regions have been proposed for jointed goatgrass control (Evans et al. 1999; Pester et al. 1999; Young et al. 2002). Integrated weed management strategies may be improved by greater understanding of dormancy cycles, agronomic influences on seed development and germination, and genetic and environmental effects on seed dormancy and production (Buhler et al. 1997; Dyer 1995; Taylorson 1987).

Studies on jointed goatgrass seed production and dormancy are few and only a limited number of populations have been investigated. The jointed goatgrass spike has three to 11 spikelets arranged alternately along a main stem. Each spikelet produces two to five florets (Hitchcock 1950; Johnston and Parker 1929; McGregor 1987), and seed are produced most often in the two lowest positioned florets (primary and secondary). Donald and Zimdahl (1987) examined seed production in two Colorado populations and reported that approximately 20% of spikelets had one seed, 80% had two seed, and less than 1% had three seed. However, they did not clarify seed production by floret or spikelet position on the spike. Differences in jointed goatgrass seed size and dormancy exist based on seed position within the spikelet (Fandrich, unpublished data; Fandrich and Mallory Smith 2003). Carpenter and Thill (1992) reported that primary positioned seed from the middle of the spike were more dormant than primary seed from the upper and lower spike regions, although further results were not published.

The upper positioned spikelets on a jointed goatgrass spike are generally the first to undergo anthesis (personal observation). It is hypothesized that seed produced at the top of the jointed goatgrass spike will be more dormant than seed produced on middle and lower regions of the spike. The first seed produced on wild oat (*Avena fatua* L.), also an annual grass weed, were shown to be the most dormant (Green and Helgeson 1957; Schwendiman and Shands 1943). The objective of this research was to quantify jointed goatgrass seed germination and production by spikelet position within the spike and floret position within the spikelet. Six jointed goatgrass populations were included in the investigation.

Materials and Methods

Seed Source

Mature spikelets of jointed goatgrass populations were collected in 2001 from winter wheat, spring wheat, and winter barley fields in north central and northeastern Oregon, and south central and southeastern Washington (Table 7.1). Spikes were clipped from the plants when the culms appeared completely dry, and shattered spikelets were collected from the soil surface near the plants. Spikes and spikelets collected within a field were designated as a single population. At Corvallis, OR, spikes were broken apart, spikelets were cleaned by hand to remove debris, and population samples were stored at room temperature (22 ± 2 C) in paper envelopes.

Table 7.1. Jointed goatgrass habitat, elevation, and location for populations collected in 2001 and grown in common garden experiments in 2002 and 2003.

Population	Habitat/type	Elevation ---- m ----	Latitude ---- ° N ----	Longitude ---- ° W ----
Athena, OR – W	Crop/winter	325	45.81	118.49
Helix, OR – S	Crop/spring	535	45.85	118.65
Helix, OR – W	Crop/winter	535	45.85	118.65
The Dalles, OR – W	Crop/winter	62	45.70	120.73
Bickleton, WA – W	Crop/winter	920	46.00	120.30
Pullman, WA – S	Crop/spring	598	46.74	117.11

Oregon and Washington source jointed goatgrass populations were grown during the 2001-02 and 2002-03 seasons in common garden nurseries at the Columbia Basin Agricultural Research Center at Pendleton, OR, the Sherman County Experiment Station at Moro, OR, and the Lewis Brown Horticultural Farm at Corvallis, OR. Spikelets were sown in areas without a history of jointed goatgrass infestation. Plants from each population were grown from 45 spikelets sown 3 cm deep into 2 m rows spaced 60 cm apart. Thirty g of slow-release, granular fertilizer[1] were evenly spread in the furrow at planting. Nurseries were weeded by hand as necessary, and no other maintenance was required.

At maturity, unbroken spikes from each jointed goatgrass population were harvested by row and stored at -30 C to minimize seed dormancy loss. Seed dormancy loss in wheat (Nyachiro et al. 2002) and wild oat (Foley 1994) were delayed by storage at -20 C. Unbroken spikes from each population were sorted according to spikelet number per spike, and were returned to cold storage. Less than 30 min per population were allotted to sort spikes. Sub-samples of unbroken spikes from each -30 C stored population were allowed to after-ripen at room temperature (22 ± 2 C) in paper bags for one year.

Germination Description and Definition

Jointed goatgrass seed do not freely separate from the glumes (Heyne 1950; Johnston and Parker 1929); rather, primary and secondary seed remain attached to the nearest glume. Because these seed may have different dormancy and germination requirements, it is necessary to distinguish between primary and secondary seed germination. Seed from the secondary positioned floret usually germinate first (personal observation; Morrow et al. 1982), and germination for these seed was defined by 3 mm of radicle emergence. A coleoptile emerges from the spikelet approximately 2 d after seed germination (personal observation). Primary positioned seed usually germinate second, and their germination can be confirmed only by emergence of a *second* coleoptile. It is not possible to distinguish between germination of the primary and secondary positioned seed based on radicle emergence alone, because this would require significant spikelet disturbance, and could interfere with germination. For more information, the reader is referred to Fandrich and Mallory-Smith (2005).

Spikelet Position on the Spike

Spikes from dormant (stored at -30 C) and non-dormant (after-ripened) samples of four Oregon and two Washington jointed goatgrass populations grown at the common garden nurseries at Pendleton, and Moro, OR were used in this experiment. Spikes composed of 9 spikelets were broken apart, and spikelets were placed according to position (1=basal spikelet and 9=terminal spikelet) into 10.2 by 10.2 cm germination boxes containing moistened ‘steel blue’ blotter paper[2]. For one population, The Dalles, OR, only spikes of spikelet length 8 were available for the study. Boxes were covered and placed in a germination chamber set to 25/15 C day/night temperatures and 12 hr photoperiod. Observations were made daily. Germination of the secondary positioned seed was recorded when approximately 3 mm of radicle emerged from the spikelet. Germination of the primary positioned seed was recorded when the second coleoptile emerged from the spikelet. Approximately 1-ml of water was added to each box every 3 d. Spikelet number varied according to available seed. No less than 22 spikelets by position were used for each test. Tests were conducted for 14 days and were repeated.

The mean germination response for each spikelet and floret position by population and dormancy type was graphed against time. There were no differences between repeated tests and data were combined. Non-linear regression models common for analysis of percent germination data were fit to the combined data. Significantly different parameters were distinguished from one another using confidence intervals (α=0.05). Data were analyzed separately for germination defined by 1) emergence of the radicle and 2) emergence of the second coleoptile. Data were combined over spikelet position when results were not significantly different.

Broken versus Unbroken Spikes

A single, after-ripened Washington origin jointed goatgrass population grown at the common garden experiment at Pendleton, OR was used in this experiment. This population was studied previously in the ‘Spikelet position’ experiment. Conditions for the germination tests were as previously described. Unbroken spikes composed of 9 spikelets were placed along parallel lines into 15.2 by 22.9 cm germination boxes containing moistened ‘steel blue’ blotter paper[3]. Germination by spikelet and floret position was recorded daily, and analyzed using non-linear regression models as described in the ‘Spikelet position’ experiment. The experiment had three replicates of eleven unbroken spikes per box, and was repeated. Data were compared to germination results obtained from broken spikes of the same population used in the ‘Spikelet position’ experiment.

Seed Production

Unbroken spikes from an Oregon jointed goatgrass population originating at The Dalles, and from a Bickleton, WA population were used to determine seed production per spikelet position on the spike, and per floret position within the spikelet. Samples from the original field collections and from the Pendleton and Corvallis, OR common garden nurseries in 2001-02 and 2002-03 were inspected for unbroken spikes. Spikes composed of 7 to 10 spikelets were broken into spikelets based on spike position. Spikelets were dissected, and seed sorted and counted according to floret position. Floret position was numbered with 'primary' at the basal end of the spikelet. Unbroken spikes were not found in the original field samples, so the bottom portion of a spike, identified by its breakage from the rachis, was used. The number of unbroken spikes per sample varied, and results are provided only when the sample size was 11 or greater. Many spikes were destroyed during harvest, and a full comparison of nursery locations, years, and spike lengths within a population was not possible. The frequencies of observing a primary, secondary, and tertiary positioned seed were calculated.

Results and Discussion

Spikelet Position on the Spike

Spikelet position and jointed goatgrass population origin affected secondary seed germination, defined as radicle emergence, in dormant samples. There were no differences in secondary seed germination by spikelet position in samples of the dormant Bickleton, WA population (Fig. 7.1). Germination began within 3 d, was rapid, and reached a maximum 94% germination by 8 d. However, spikelet position affected germination in the dormant Athena, OR population. Seed from spikelet positions 1 to 6 germinated earlier, faster, and to a greater final percent than seed from positions 7, 8, and 9 (Fig. 7.1). Spikelet position affected days to germination and final germination percent, but not rate, in the dormant The Dalles, OR population (Fig. 7.1). Spikelet position and population affected also primary seed germination, defined as emergence of the second coleoptile, in dormant samples. In a Bickleton, WA dormant sample, more seed germinated from positions 2, 3, and 4 than seed from positions 1 and 5 to 7 (Fig. 7.2).

Days to germination and germination rates among primary positioned seed in these spikelet positions were similar. Primary seed did not germinate in the other two dormant populations. Germination of tertiary seed was affected by spikelet position and population; 15% of tertiary seed in spikelet position 2 of the dormant Bickleton, WA population germinated (Fig. 7.3). Tertiary seed did not germinate in the other dormant populations.

Neither spikelet position nor population affected secondary seed germination in after-ripened samples (Fig. 7.4). Germination began within 3 d, was rapid, and was complete by 6 d. Germination patterns of spikelets stored at -30 C in Fig. 7.1 compared to after-ripened spikelets in Fig. 7.4 confirm that the absence of germination in -30 C stored samples was attributed to innate seed dormancy and not inadequate testing conditions or non-viable seed. Although secondary seed in dormant spikelets of the Bickleton, WA population germinated to nearly 100% by the end of the test (Fig. 7.1), the germination rate for these seed was slower than the rate in the after-ripened sample.

Spikelet position and jointed goatgrass population affected primary seed germination in after-ripened populations. In the Bickleton, WA after-ripened population, more coleoptiles emerged from positions 1 through 4 compared to positions 5 through 9 (Fig. 7.5). In the Pullman, WA after-ripened population, more coleoptiles emerged from positions 1 to 8 than from position 9 (Fig. 7.5). In the Helix, OR after-ripened population, more coleoptiles emerged from positions 1 to 7 than from positions 8 and 9 (Fig. 7.5). Because the onset to germination and germination rates for the different spikelet positions among jointed goatgrass populations were similar, differences in final germination values may have resulted from different seed numbers rather than dormancy.

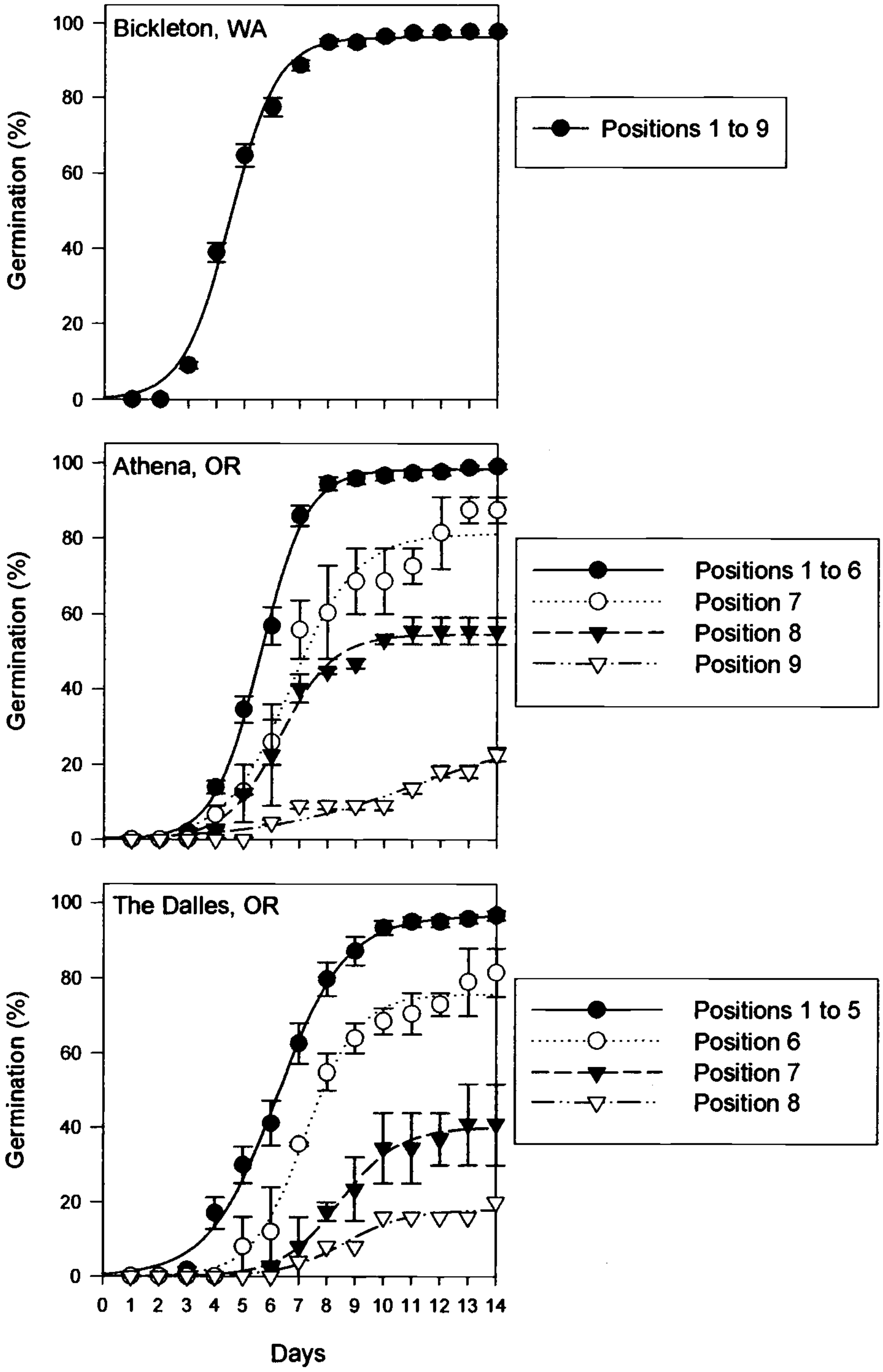

Figure 7.1. Germination, defined as radicle emergence, by spikelet position in three dormant jointed goatgrass populations. Lines represent predicted values; symbols represent means with standard error bars.

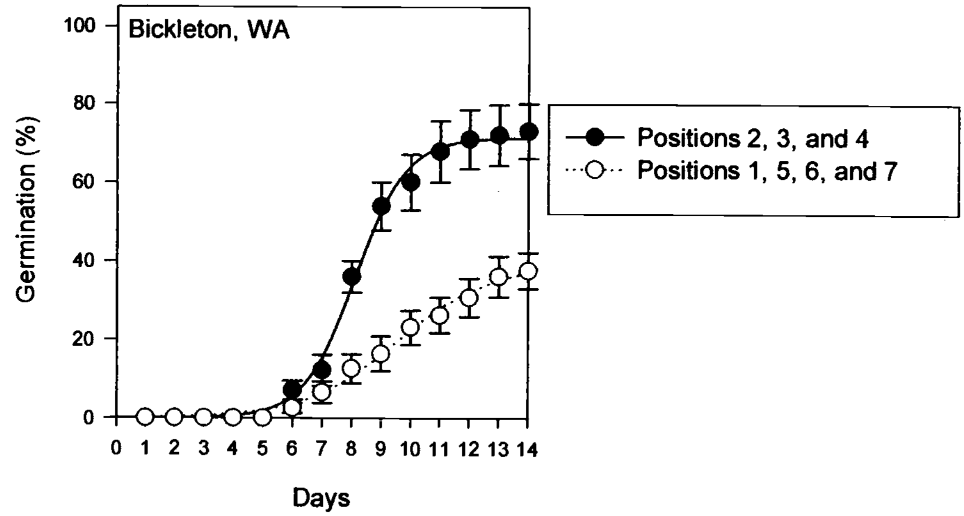

Figure 7.2. Germination, defined as emergence of the second seedling, grouped by spikelet position in a dormant, Bickleton, WA jointed goatgrass population. Lines represent predicted values; symbols represent means with standard error bars.

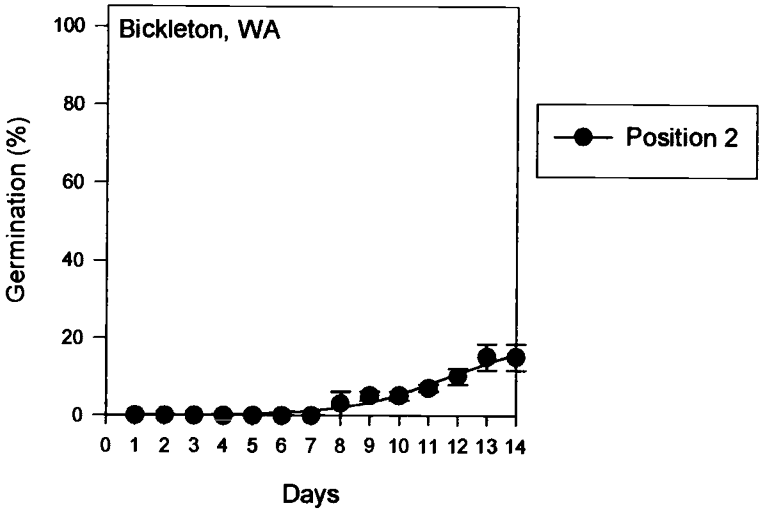

Figure 7.3. Germination, defined as emergence of the third seedling, grouped by spikelet position in a dormant, Bickleton, WA jointed goatgrass population. Lines represent predicted values; symbols represent means with standard error bars.

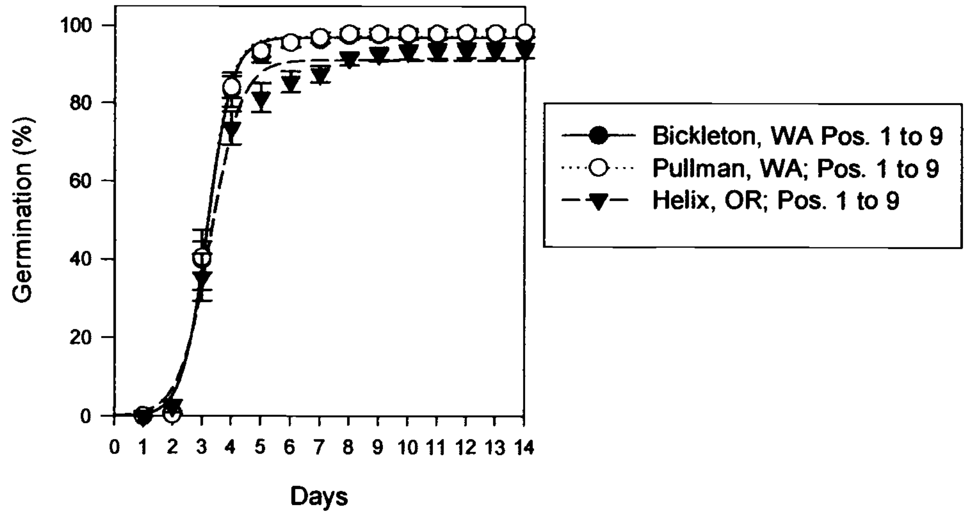

Figure 7.4. Germination, defined as radicle emergence, averaged over spikelet positions 1 to 9 in three after-ripened jointed goatgrass populations. Lines represent predicted values; symbols represent means with standard error bars.

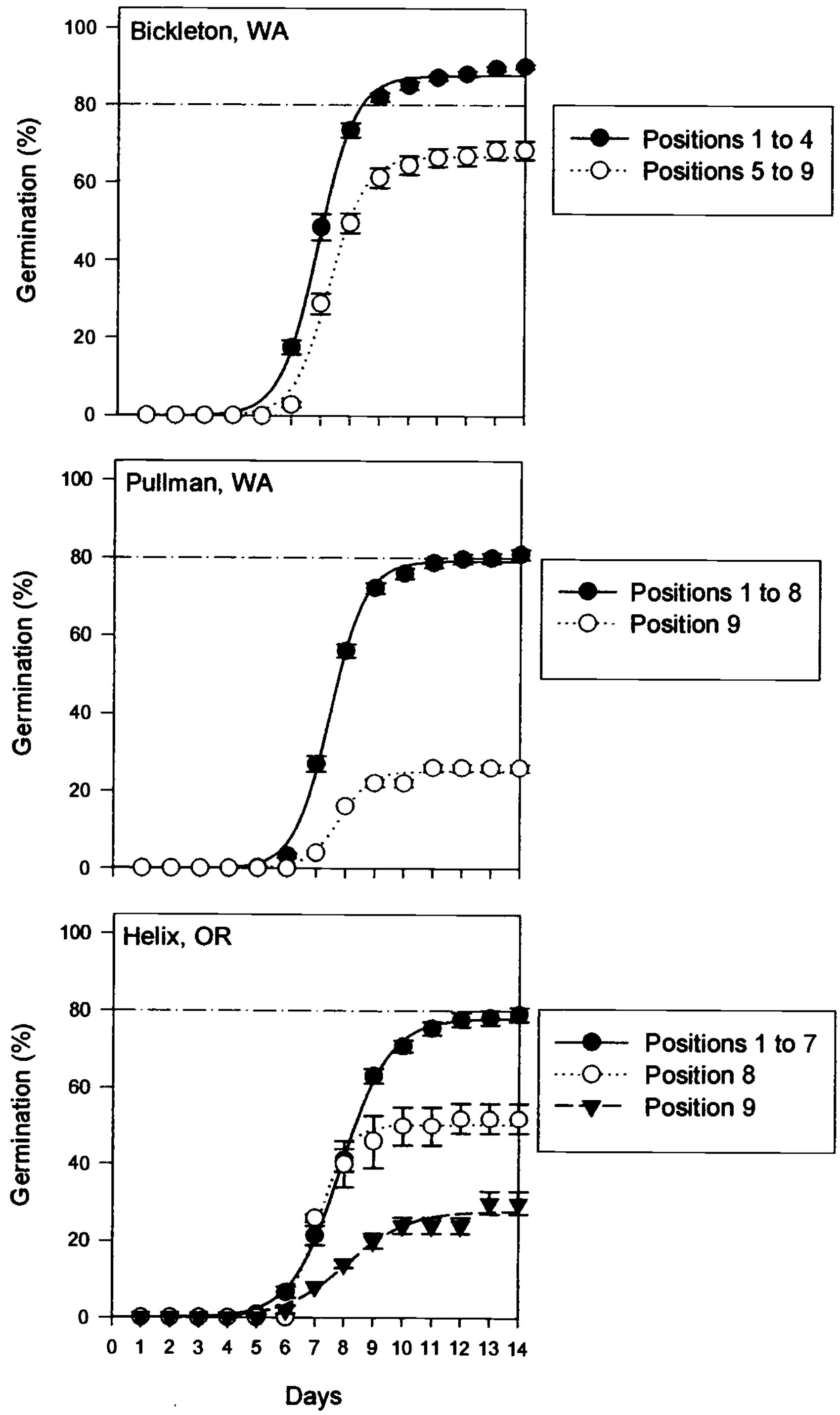

Figure 7.5. Germination, defined as emergence of the second seedling, grouped by spikelet positions in three after-ripened jointed goatgrass populations. Lines represent predicted values; symbols represent means with standard error bars. A line at 80% germination represents a theoretical maximum germination based on seed counts of Donald and Zimdahl (1987).

An unexpected result in these experiments was the abundance of spikelets in a single after-ripened jointed goatgrass population of spike length 9 to produce three coleoptiles. In the Bickleton, WA after-ripened population, 67% of spikelets in positions 2 and 3 yielded three coleoptiles (Fig. 7.6). It was reported previously that less than 1% of jointed goatgrass spikelets contained three seed (Donald and Zimdahl 1987). Final germination values based on the third coleoptile were affected by spikelet position (Fig. 7.6). More seed from positions 2 and 3 germinated than from positions 1, 4, and 5. Tertiary seed germination rates based on spikelet position were not different, but seed from spikelet position 5 were the last to germinate. Spikelets in positions 6, 7, 8, and 9 did not produce three seed (data not shown).

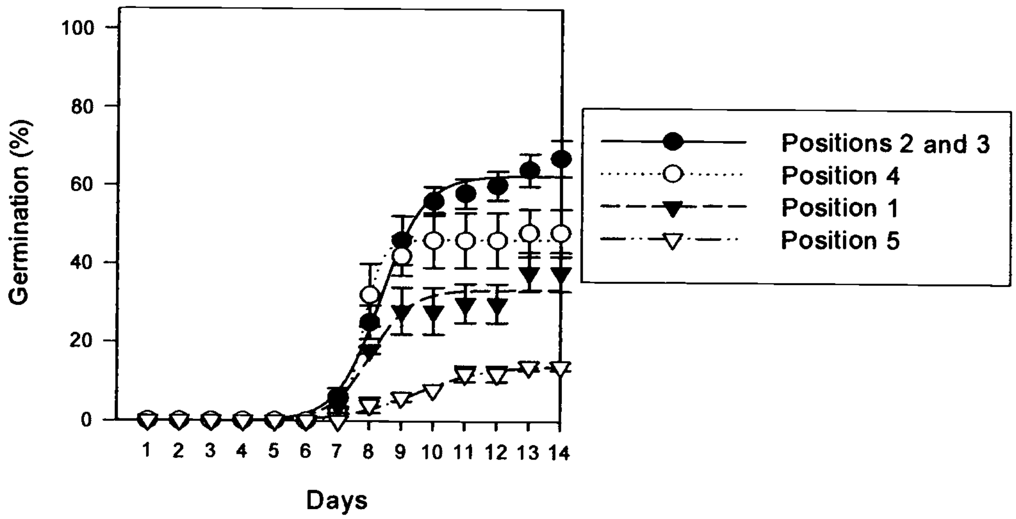

Figure 7.6. Germination, defined as emergence of the third seedling, grouped by spikelet position in an after-ripened, Bickleton, WA jointed goatgrass population. Lines represent predicted values; symbols represent means with standard error bars.

Broken versus Unbroken Spikes

Final germination values for secondary positioned seed within the spikelet were not affected by breaking the spike into individual spikelets. However, secondary seed in spikelet positions 1 through 9 germinated more rapidly and germination started 2 d earlier in broken spikelets than seed from unbroken spikes (Table 7.2). Germination of the primary positioned seed within jointed goatgrass spikelets also began 2 d earlier in broken spikes than in unbroken spikes. We hypothesize that an unbroken spike arrangement may restrict penetration by the radicle and slow the onset of germination.

Table 7.2. Predicted values and confidence intervals (α=0.05) for seed germination maximum values, rates, and lags using spikelets imbibed as unbroken and broken jointed goatgrass spikes.

	Unbroken spikes				Broken spikes			
		Estimate	LCLM[b]	UCLM[b]		Estimate	LCLM[b]	UCLM[b]
Variable[a]			%				%	
M	Secondary[c]	94	92	96	Secondary	97	96	98
K	Pos.[d] 1 to 8	1.4	1.1	1.5	Pos. 1 to 9	2.4	2.1	2.7
L		5.2	5.0	5.3		3.2	3.1	3.2
M	Secondary	91	83	98				
K	Pos. 9	1.1	0.5	1.5				
L		6.6	6.1	7.1				
M	Primary[e]	65	62	67	Primary	79	77	81
K	Pos. 1 to 8	1.8	1.4	2.0	Pos. 1 to 8	1.7	1.3	1.9
L		9.9	9.8	10.0		7.5	7.3	7.5
M	Primary	30	28	33	Primary	25	24	26
K	Pos. 9	2.1	1.2	2.9	Pos. 9	1.9	1.2	2.4
L		10.8	10.5	11.0		7.8	7.6	7.9

[a] M=predicted maximum germination; K=germination rate; L=days to germination.

[b] Lower and upper confidence limits on the predicted values.

[c] Presence of the radicle; assumed from secondary positioned seed.

[d] Spikelet position where 1=basal and 9=terminal.

[e] Presence of the second coleoptile; assumed from primary positioned seed.

In unbroken spikes only, secondary seed within spikelet position 9 required one additional day to begin germination compared to secondary seed in positions 1 to 8. In both unbroken and broken spikes, less primary seed germinated in spikelet position 9 than primary seed in positions 1 to 8. However, days to the onset of germination and germination rates among primary seed in spikelet positions 1 through 9 were similar. Because germination onset and lags were similar, differential final primary seed germination values for spikelet position on the spike may indicate that less seed are produced at the top of the spike rather than an influence of seed dormancy.

Seed Production

Jointed goatgrass seed developed in all three positioned florets of spikelets collected at the original field sites. However, more seed were produced in primary and secondary positioned florets compared to tertiary florets (Table 7.3), and some spikelets did not contain a tertiary seed. Seed were not preferentially produced in primary or secondary positioned florets in 2001 field samples. Dissection confirmed that the frequency of observing a seed in tertiary positioned florets was greater for the Bickleton, WA population than the population from The Dalles, OR.

Table 7.3. Percent seed production by spikelet and floret position for two jointed goatgrass populations collected from fields in Oregon and Washington in 2001. Spikelet position was numbered with '1' at the basal end of the spike. Primary, secondary, and tertiary refer to floret position with primary at the basal end of the spikelet.

	The Dalles, OR - 2001			Bickleton, WA - 2001		
	Length unknown			Length unknown		
	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.
Spikelet	---------------------- % ----------------------					
1	72	60	0	88	84	48
2	76	84	8	96	88	56
3	72	80	4	88	96	44
4	80	56	0	96	80	28

Because spikelets were gathered from plants grown in two environments, the relative contributions of environment and genetics on differential seed production values for the original Oregon and Washington jointed goatgrass collections could not be distinguished. However, greater seed production in tertiary florets of the Washington population compared to the Oregon population was observed also when the populations were grown together in common garden experiments (Table 7.4). Furthermore, this event occurred across years (Table 7.5) and nursery locations (Table 7.6). Seed production within spikelets may be influenced also by spikelet position on the spike. Seed production in tertiary florets was observed most often in the bottom four positioned spikelets. Seed production in secondary florets was frequent in nearly all spikelet positions on the spike, but it occurred less often in the terminal spikelet. Because drying of jointed goatgrass spikes and spikelets occurs in a basipetal direction, fertilized ovules in lower positioned spikelets on a spike and florets within a spikelet may have longer access to water and nutrients, and subsequently, a greater potential exists for seed development compared to ovules at the top of the spike and spikelet.

Table 7.4. Percent seed production by spikelet and floret position for two jointed goatgrass populations grown in a Pendleton, OR field nursery during 2001-02. Spikelet position was numbered with '1' at the basal end of the spike. Primary, secondary, and tertiary refer to floret position with primary at the basal end of the spikelet.

	The Dalles, OR – 2001-02						Bickleton, WA – 2001-02					
	Length=7			Length=8			Length=7			Length=8		
	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.
Spikelet	%											
1	73	100	0	93	79	7	96	92	60	96	100	32
2	100	82	9	86	93	21	92	96	68	92	92	52
3	91	100	0	93	71	7	88	96	56	96	92	56
4	91	91	9	100	93	0	96	96	8	92	96	20
5	100	82	0	86	71	7	96	100	4	100	92	8
6	100	45	9	79	93	0	96	92	0	100	92	0
7	91	9	0	65	64	0	92	68	0	92	96	0
8	n/a	n/a	n/a	65	14	0	n/a	n/a	n/a	92	72	0

Discontinuous germination is one characteristic from a list of several adaptive and polymorphic traits that contribute to the success of weed (Baker 1974). As a result, a portion of seed may germinate at a given time or place specific to the survival of the seedling and adult plant, and in general to the survival of the population. Within the Poaceae family, the degree of polymorphism associated with seed dormancy varies widely (Baskin and Baskin 1998; Simpson 1990). Seed dormancy may vary among populations (Evans and Cabin 1995; Frost and Cavers 1975; Naylor and Abdalla 1982; Paterson et al. 1976), and seed from the same plant may have different levels of dormancy (Dekker et al. 1996; Gutterman 1985, 1992). Jointed goatgrass typically displays a winter annual life history and seed production is the only method of reproduction. Differential seed dormancy based on position within the inflorescence has distinct ecological advantages and may serve to lengthen the time and/or broaden the conditions over which jointed goatgrass seed may germinate.

Table 7.5. Percent seed production by spikelet and floret position for two jointed goatgrass populations grown in a Pendleton, OR field nursery during 2002-03. Spikelet position was numbered with '1' at the basal end of the spike. Primary, secondary, and tertiary refer to floret position with primary at the basal end of the spikelet.

	The Dalles, OR – 2002-03											
	Length=7			Length=8			Length=9			Length=10		
	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.
Spikelet	%											
1	88	96	8	100	96	12	80	76	0	100	89	0
2	88	96	12	92	96	24	88	92	20	100	94	11
3	88	96	12	88	88	20	80	92	40	94	100	22
4	100	92	4	96	92	12	96	88	4	78	94	11
5	92	96	4	96	80	4	84	88	8	100	94	17
6	84	84	0	92	88	4	88	92	0	94	89	0
7	96	72	0	80	84	0	88	76	0	83	83	0
8	n/a	n/a	n/a	92	36	0	88	68	0	83	83	0
9	n/a	n/a	n/a	n/a	n/a	n/a	84	32	0	89	61	0
10	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	89	11	0

Table 7.5 (Continued). Percent seed production by spikelet and floret position for two jointed goatgrass populations grown in a Pendleton, OR field nursery during 2002-03. Spikelet position was numbered with '1' at the basal end of the spike. Primary, secondary, and tertiary refer to floret position with primary at the basal end of the spikelet.

	Bickleton, WA – 2002-03											
	Length=7			Length=8			Length=9			Length=10		
	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.
Spikelet	%											
1	83	100	0	100	92	36	96	100	56	92	96	32
2	92	75	17	92	92	40	92	92	80	92	88	80
3	100	92	8	96	96	28	92	84	64	100	84	76
4	92	83	0	92	100	8	88	92	32	100	92	68
5	83	92	8	96	96	0	84	96	0	92	84	40
6	92	75	0	92	84	0	96	96	0	84	92	16
7	75	42	0	88	92	0	88	88	0	92	100	4
8	n/a	n/a	n/a	100	68	0	96	84	0	92	92	0
9	n/a	n/a	n/a	n/a	n/a	n/a	100	80	0	84	88	0
10	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	92	88	0

Table 7.6. Percent seed production by spikelet and floret position for two jointed goatgrass populations grown in a Corvallis, OR field nursery during 2002-03. Spikelet position was numbered with '1' at the basal end of the spike. Primary, secondary, and tertiary refer to floret position with primary at the basal end of the spikelet.

	The Dalles, OR – 2002-03						Bickleton, WA – 2002-03					
	Length=8			Length=9			Length=8			Length=9		
	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.	Pri.	Sec.	Ter.
Spikelet	%											
1	76	76	0	82	86	14	92	84	36	95	100	21
2	90	81	10	95	73	9	80	92	44	100	100	42
3	86	86	5	91	95	27	92	88	8	100	100	26
4	86	90	0	95	86	32	92	76	0	89	95	16
5	71	71	10	86	91	18	96	88	4	95	100	0
6	81	71	0	91	86	5	88	88	0	100	100	0
7	86	33	0	95	68	5	72	80	0	100	84	0
8	86	24	0	82	55	0	84	36	0	89	53	0
9	n/a	n/a	n/a	95	32	0	n/a	n/a	n/a	100	42	0

Spikelet position, combined with the effects of environment during seed maturation and the age of the plant at seed development, accounts for a great deal of the variability among weed populations known to exhibit large variations in germination (Andersson and Milberg 1998). Efforts to model the life history of jointed goatgrass and predict germination should be adjusted to account for these effects. In addition, models that predict seed rain in a context where spikes shatter and/or a portion of the spike is harvested with winter wheat should account for differential seed production based on inflorescence position. The scope of germination patterns revealed by six populations of jointed goatgrass in these experiments emphasizes the complexities involved when designing and interpreting seed production and germination tests. We suggest that future research include sampling seed from several populations, and an effort be made to standardize germination tests according to seed position on the inflorescence. Additional research needs to be conducted to study environmental influences on seed development within the spike and spikelet. Seed with different germination patterns should be tested also for seedling vigor.

Sources of Materials

[1] Osmocote 14-14-14. The Scotts Company, 14111 Scottslawn Road, Marysville, OH 43041.

[2] BB44 Steel Blue Blotter. Hoffman Manufacturing Inc., International Agri-Supply, 353 29th Avenue SW, Albany, OR 97321.

[3] BB69 Steel Blue Blotter. Hoffman Manufacturing Inc., International Agri-Supply, 353 29th Avenue SW, Albany, OR 97321.

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Vernalization Requirements and Seed Dormancy
of Jointed Goatgrass (*Aegilops cylindrica*)

CHAPTER 8

General Conclusions

Quantification of winter wheat and jointed goatgrass vernalization requirements was necessary to predict the conditions under which jointed goatgrass plants could establish and be available for crossing with wheat. In field studies, jointed goatgrass plants required more vernalization to produce spikelets and germinable seed than 'Madsen' (Allan et al. 1989) winter wheat plants. However, once minimum vernalization thresholds were met, jointed goatgrass and winter wheat yields responded similarly to increasing vernalization days. In greenhouse studies, plants of jointed goatgrass populations collected from Oregon and Washington wheat fields required fewer vernalization days to reach the joint stage than plants of Madsen winter wheat. However, jointed goatgrass populations were polymorphic for this reproductive response, and plants of a Washington roadside population required a longer vernalization period than Madsen plants to reach a similar stage. A confounding factor in modeling jointed goatgrass vernalization requirements was revealed by the longer period between jointing and anthesis observed in the greenhouse in Oregon and Washington winter and spring jointed goatgrass populations compared to the Washington roadside population and Madsen winter wheat. In summary, a 6-wk vernalization duration represents the minimum requirement for synchronous reproduction among a jointed goatgrass population, Madsen winter wheat, and Madsen by jointed goatgrass hybrids, yet the risk of gene transfer might be greater when the onset of reproductive development is most similar - after 7-wk vernalization.

Specific vernalization conditions, limited temperature variability, and more detailed observations in the greenhouse vernalization study revealed reproductive differences among jointed goatgrass populations not observed in field studies. The large scale of the field research study restricted observations on reproductive biology to spike production and germinable seed. As such, field observations on GDD to early reproductive development (joint stage) and quantification of the period between jointing and anthesis were lacking. Furthermore, an "all or nothing" approach to reproductive development based on the presence or absence of spikes at harvest may have overestimated synchronous development among the jointed goatgrass populations. The experimental design of the field study may be improved by reducing the number of populations to those with the greatest difference in vernalization response, taking measurements of GDD to the joint stage, and following with the measurement of GDD to 50% heading to support these data.

There was not selection for a spring-type growth habit in the jointed goatgrass populations tested. However, if spring temperatures were cool, plants may be vernalized and complete their life cycle before the end of the growing season. Therefore, a spring crop rotation might reduce, but not eliminate, jointed goatgrass infestations as part of an integrated weed-management plan. Because spring wheat and jointed goatgrass have been observed nicking during anthesis in Oregon fields (Morrison et al. 2002), spring cropped fields should be scouted for wheat by jointed hybrid plants, and these plants removed before seed production and dissemination. This practice ensures also that producers receive the maximum weed-management benefit of planting spring crops.

Detailed studies of jointed goatgrass seed dormancy in response to environmental and genetic influences can be used to improve the effectiveness of integrated weed-management strategies. Germination of freshly harvested jointed goatgrass seed promoted by low temperatures was similar to Gleichsner (1987) and Morrow et al. (1982). Thermal dormancy prevents germination during the summer, even if rain wets the soil, because soil temperatures are above those required for germination. Dormancy in jointed goatgrass might prevent germination of seed within freshly shattered spikelets until autumn when temperatures are low and moisture is available. Additionally, research presented herein clarified that jointed goatgrass seed germinated better with alternating temperature regimes compared to constant regimes. Lack of germination only at unfavorable temperatures represents a minimum or low level of dormancy (Taylorson

1987), while a requirement for a diurnal change from a lower to a higher temperature, as in the case of jointed goatgrass, represents a greater level of dormancy. The short dormancy periods for secondary and primary seed in jointed goatgrass suggest that nearly all of the seed would germinate in the fall or spring after shattering if moisture were available. Our results predict that jointed goatgrass should exhibit a transient seed bank, with seed turnover of less than one year (Grime 1981). However, because final germination percentages in jointed goatgrass primary and secondary seed were less than 100%, additional research on factors regulating dormancy is needed.

Genetic control and environmental influences contributed to the variation in jointed goatgrass vernalization response, dormancy and germinability, and likely contributes to the adaptability of jointed goatgrass in variable habitats across as the western United States. The persistence of jointed goatgrass populations would be favored by an extended and/or non-synchronous reproductive period. Jointed goatgrass seed produced under a wide range of environmental conditions might have different germination requirements, thus insuring population survival over time. In fact, our research confirmed polymorphism for seed germination among jointed goatgrass populations. Because the original seed populations were collected within a limited geography and from fields with similar crop histories, it is hypothesized that vernalization and germination differences among populations do not reflect selection for different ecotypes. Rather, reproductive variability might be part of a general purpose genotype strategy to promote germination and colonization in a wide range of environments (Silvertown and Charlesworth 2001).

Future research on jointed goatgrass management should include populations collected from diverse geographic and agronomic origins. To isolate the effects of environment on growth and reproductive development, populations should be grown in common garden experiments. Additional research ideas posed by the studies conducted herein include: 1) determination of seedling vigor and competition among seedlings germinated from seed produced at different times in the growing season, i.e., under different vernalization conditions; 2) quantification of seed size for seed developed within the same spikelet; 3) determination of seedling vigor and competition among seedlings germinated from seed differentially positioned within the same spikelet; 4) determination of the environmental factors that contribute most to heteroblastic seed development; 5) determination of the environmental factors that contribute most to the selection of jointed goatgrass populations with differing phenotypes and/or genotypes; and 6) identification of the genes that regulate vernalization response. Experiments in the aforementioned topics would clarify the competitive effects of jointed goatgrass plants from seed produced under a broad range of environmental conditions, identify conditions with greatest risk for selection of biotypes adapted to management strategies, confirm population polymorphism for vernalization response, and lead to site-specific management recommendations.

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