Vernalization Requirements for Flowering of Jointed Goatgrass (Aegilops cylindrica)¹

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Abstract. Jointed goatgrass (Aegilops cylindrica Host. #3 AEGCY) has a quantitative requirement for vernalization in order to flower. In greenhouse and field studies, increasing periods of vernalization progressively reduced the number of days needed for plants to mature following transfer from the cold treatment to favorable growing conditions. Plants that had been vernalized at 3 ± 2 C for 8 weeks as imbibed seed took 120 days to flower following transfer to the greenhouse. Unvernalized controls flowered 197 to 222 days after planting in the greenhouse. Lengthening periods of vernalization from 2 to 8 weeks increased the number of seedheads per plant and dry weight per seedhead. Vernalized plants partitioned more dry matter into seedheads than unvernalized controls. The ratio of seedhead dry weight to vegetative shoot dry weight increased with duration of vernalization, even though vernalization did not alter total shoot dry-matter production. In field studies, plants that were established in the fall flowered sooner and more synchronously after resumption of growth in the spring than those that were planted in the spring and flowered in the summer. Plants seeded after May failed to flower in the same summer.

Additional index words: Anthesis, grass weed, temperature, AEGCY.

INTRODUCTION

Jointed goatgrass is well adapted to stubble-mulch tillage in the winter wheat (Triticum aestivum L. #TRZAX)-fallow rotation of the Central Great Plains (8, 13). As stubble-mulch tillage has become more common for residue management and erosion control, so have many grass weeds of winter wheat, such as downy brome (Bromus tectorum L. #BROTE) and jointed goatgrass. Jointed goatgrass and winter wheat are related genetically and share the D-chromosome (23). Because of this genetic similarity, attempts to selectively control jointed goatgrass in winter wheat with herbicides have failed (7). However, there are some herbicides that can be used to control jointed goatgrass, volunteer wheat, and other grass species in chemical fallow (7, 8, 9, 10, 11, 14). While jointed goatgrass can be controlled with herbicides in other crops, these crops cannot be grown profitably

Jointed goatgrass germinates with winter wheat in the fall and to a lesser extent in the spring. Its vegetative and reproductive growth mirrors that of winter wheat so that at harvest its seedheads are close to the height of the seedheads of wheat. Some seed shatter before harvest, but others are combined with the wheat. The seed of this species is difficult to remove from grain by conventional methods of seed cleaning. Thus, this weed reduces both wheat yield and quality. Other aspects of the biology and control of this species have been summarized (8, 13).

The literature on vernalization requirements for flowering has been reviewed extensively (1, 5, 12, 19, 20, 22, 35). Vernalization, or chilling, is a precondition for flowering, but floral primordia generally do not form during cold treatment. Chilling hastens the flowering of plants when conditions become inductive for floral initiation. Vernalization merely confers responsiveness to stimuli that initiate flowering, as has been demonstrated for winter wheat cultivars (15, 26, 29). Vernalization requirements may be qualitative if they have an all-or-none effect. Alternatively, they may be quantitative if they simply hasten later floral initiation. Vernalization can only be measured as an aftereffect following the end of a cold treatment.

In the field, fall-germinating species are exposed to cold temperatures as both established seedlings and imbibed seed. Seed imbibition is a prerequisite for responsiveness to cold treatment (5). Some species cannot be vernalized as imbibed seed and must first produce a certain amount of vegetative growth as seedlings. For example, reed canarygrass (*Phalaris arundinacea* L. # TYPAR) must undergo a juvenile vegetative phase before it can be vernalized (16). Those plants with a quantitative (facultative) requirement can be vernalized as imbibed seed, whereas those with a qualitative (obligate) requirement must undergo a juvenile phase prior to cold treatment (3).

The reproductive biology of grass weeds of winter wheat remains largely unexplored. Winter wheat is a qualitative long-day plant with a requirement for vernalization (26). The flowering of several fall-germinating, winter annual weeds of winter wheat is accelerated by chilling. These include downy brome (14), darnel (Lolium temulentun L. # LOLTE) (28), prickly lettuce (Lactuca serriola L. # LACSE) (30), rye (Secale cereale L. # SECCE) (5), skeleton weed (Chondrilla juncea L. # CHOJU) (4, 6), slender oat (Avena barbata Pott. ex Link. # AVEBA) (27), and field pennycress (Thlaspi arvense L. # THLAR) (24). The goal of this series of greenhouse and field experiments was to better understand some aspects of vernalization requirements for flowering of jointed goatgrass.

on dryland in the Central Great Plains because of limited seasonal rainfall. A better understanding of the biology of this weed may suggest a way to manage it in the winter wheatfallow rotation.

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MATERIALS AND METHODS

Vernalization of imbibed seed. The objectives of this experiment were to establish whether jointed goatgrass required vernalization in order to flower and whether imbibed seed could be vernalized. Jointed goatgrass seed was gathered north of Genoa, CO, and propagated at Fort Collins, CO, in 1980. Nondormant jointed goatgrass seed were placed in 8.5 - cm - diam petri dishes containing filter-paper disks moistened with deionized water. The dishes were wrapped in aluminum foil to exclude light and the seed were kept moist by periodic addition of deionized water. Jointed goatgrass seed were chilled in a dark coldroom at $3 \pm 2 C$ for 0, 2, 4, 6, or 8 weeks prior to transplanting into a potting soil. Vernalization treatments were staggered so that each was terminated at the same time. Unvernalized seed were also planted in the greenhouse at 2-week intervals at the same time that the vernalized treatments were first chilled in the coldroom.

At the end of vernalization, the 8-, 6-, and 4-week-old vernalized seed had germinated, but the 2-week-treated seed had not germinated. Seed or seedlings were allowed to acclimate at room temperature for 2 days prior to seeding or transplanting. Three uniform seedlings were transplanted into each pot (16.5 cm diam by 18 cm, 2.8 L of soil). Potted plants were fertilized with a slow-release granular fertilizer (3:1:1, N:P:K) and were watered as needed. The potting mixture was 73% sand, 19% silt, and 8% clay, and contained 3.6% organic matter at pH 7.9. After establishment, the plants were thinned to one plant per pot.

The dates of planting, seedling emergence, and the first emergence of the awns through the boot were recorded. The time of awn emergence was chosen as a relative measure of the rate of flowering and was checked three times each week. The exact time of floral initiation can be determined only by microscopic observation of dissected shoot apices following repeated destructive sampling over time. Observation of awn emergence does not discriminate between the component processes of flowering, such as floral initiation and later floral development. It also overestimates the time that plants remain vegetative. It was assumed that the rates of awn emergence and both floral initiation and development were influenced alike by vernalization (3).

Plants vernalized as seed were harvested 272 days after the end of the cold treatment, and the number of seedheads per plant, the total seedhead dry weights, and the vegetative shoot dry weights were determined. Thus, plants that had been vernalized for 0, 2, 4, 6, or 8 weeks were 272, 286, 300, 314, or 328 days old at harvest, respectively. The respective, unvernalized controls were also 272, 286, 300, 314, or 328 days old at harvest. As seedheads matured, they were removed, oven dried at 70 C for 48 h, and weighed. Dry weight per seedhead was calculated by dividing the total dry weight of the seedheads by the number of seedheads per plant.

This and the next greenhouse experiment were conducted concurrently from August 1981 to June 1983. Sunlight was supplemented with fluorescent lighting to provide at least a 14-h photoperiod throughout the year. This day length induced flowering in jointed goatgrass (3, 33). The

light irradiance and photosynthetically active radiation of the fluorescent lighting at plant height, 40 to 75 cm below the fluorescent bulbs, ranged between 20 and 68 W/m² and between 90 and 168 μ E·m⁻²·s⁻¹, respectively. The temperature varied seasonally over the course of the experiments. Throughout the winter, when most experiments were conducted, the day temperatures ranged between 18 and 28 C and the night temperatures between 15 and 20 C. The relative humidity ranged between 28 and 75% depending upon the season.

A completely randomized design was used for all greenhouse and field experiments. All three experiments were repeated once in their entirety. There were 15 plants per treatment (replications) in the first experiment. The pooled data were subjected to analysis of variance and regression analysis (17, 34).

Duration of vernalization of seedlings. This trial differed from the previous one in that the effect of various durations of vernalization outdoors on the flowering behavior of established seedlings was examined, rather than imbibed seed. The objective of this field experiment was to determine the effect of various periods of near-freezing temperatures on the flowering behavior of jointed goatgrass plants. Plants were established outdoors in pots in August and taken into the greenhouse at monthly intervals throughout the winter. The two replicates were seeded on August 4, 1981 and 1982, in order to minimize the effect of seasonal changes in photoperiod and weather. One hundred and forty pots of jointed goatgrass were started outdoors in Fargo, ND, 273 m above sea level, at a latitude and longitude of 46° 54' north and 96° 48' west, respectively. Twenty to 30 nondormant seeds were sown 2.5 cm deep in a potting soil, as described previously. Before the onset of winter, plants were thinned to 4 seedlings per pot and were watered as needed. At the same time that plants were started outdoors, seed were sown in 20 pots in the greenhouse. At monthly intervals from August to February, 20 pots of vernalized jointed goatgrass were brought indoors and thinned to one plant per pot. At the same time, an additional 20 unvernalized controls were started in the greenhouse. Maximum and minimum air temperatures were obtained from an official weather station near the experimental site. The experimental design, statistical analysis, and measured parameters were the same as in the previous experiment.

Season of establishment of seedlings. This field experiment was designed to determine the effect of date of planting on the portion of the population that flowered and the duration of flowering. At monthly intervals from August 1981 to July 1983, 20 pots of jointed goatgrass were planted outdoors. The site, environmental conditions, potting soil, and planting procedure were the same as in the previous experiments. Following establishment in the fall, the pots were thinned to four seedlings per pot. Only plants that were started from August to November emerged in the fall. In the spring, the fall plantings and all subsequent plantings that emerged were thinned to one seedling per pot. The date of seedling emergence and awn emergence through the boot was observed three times each week. Analysis

of variance could not be performed because jointed goatgrass planted from December to April failed to emerge well in the spring and the flowering data had nonuniform variance. Sample statistics were presented instead.

RESULTS AND DISCUSSION

Vernalization of imbibed seed. Low-temperature treatment of imbibed jointed goatgrass seed modified the maturation and flowering biology of this weed in the greenhouse. As the duration of cold treatment increased from 2 to 8 weeks, there was a linear decrease in the time that seedlings later spent as vegetative plants (Figure 1). Imbibed seed that had been vernalized for 8 weeks flowered 130 days after transfer to favorable growing conditions, whereas unvernalized controls flowered in about 200 days.

The flowering behavior of unvernalized plants started at 2-week intervals suggested that jointed goatgrass has a quantitative requirement for vernalization in order to flower (Table 1). Unvernalized plants needed more time to mature than plants that were cold treated as imbibed seed even when the period of vernalization was considered. In the greenhouse, unvernalized plants took between 197 ± 2 and 222 ± 7 days (mean ± SE) to flower. This period of active vegetative growth was longer than that of cold-treated plants (Figure 1 and Table 1). The relationship between plant age at harvest and days required to flower was linear for unvernalized plants (P = 0.0001, $r^2 = 0.35$). Apparently, date of planting in the greenhouse influenced the time that unvernalized jointed goatgrass plants needed to flower, contrary to expectations (Table 1). Perhaps seasonal changes in greenhouse temperature, photoperiod, or light quality

In addition to increasing the rate of plant maturation, longer periods of cold treatment caused progressive increases in the number of seedheads per plant at 272 days after transplanting (Figure 2). Jointed goatgrass that had been vernalized for 8 weeks produced nearly three times as many seedheads as the unvernalized controls.

As unvernalized plants aged, they continually formed more seedheads per plant (Table 1). Plants that were vernalized for 8 weeks and allowed to grow in the greenhouse for 272 days formed 51.5 ± 3.6 seedheads per plant. Unvernalized plants that had grown for 328 days formed an equivalent number, 46.7 ± 6.4 seedheads per plant. Younger unvernalized plants formed fewer seedheads per plant (Table 1). The plants that were vernalized for 8 weeks and grown for 272 days in the greenhouse were the same chronological age as the unvernalized controls, 328 days old.

As the duration of cold treatment increased, the dry weight per seedhead also increased (P = 0.0001) (Figure 3). Seedhead weight is a fairly good estimate of reproductive dry weight because the seedhead disarticulates into individual dispersal units leaving no spike (8). Even though vernalized and unvernalized plants of the same chronological age had the same number of seedheads per plant, their dry weight per seedhead was 0.13 and 0.22 g, respectively. Thus, the cold treatment had a morphogenic effect and did not simply delay vegetative growth while permitting progress toward reproductive ma-

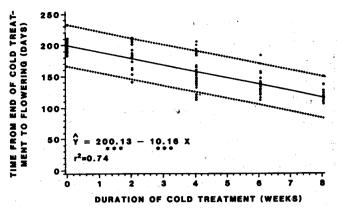


Figure 1. The effect of the duration of vernalization on the time from the end of the cold treatment to flowering of jointed goatgrass growing in the greenhouse. The best fitting regression equation and 95% confidence interval are presented for the pooled data. The stars indicate that the intercept and coefficients were significantly different from zero (P<0.0001).

turity. The dry weight of individual seedheads of unvernalized plants was not changed greatly as plants aged (Table 1). In contrast, the dry weight per seedhead increased as the period of chilling lengthened, so that it was 1.7 times greater for vernalized plants than for unvernalized plants that were 328 days old. However, because the seed development of plants of the same chronological age did not occur at the same time, these differences may also be related to other factors, such as environment.

Even though vernalized plants flowered in less time, formed more seedheads per plant, and accumulated more dry weight per seedhead, the total shoot dry matter was uninfluenced by the duration of vernalization (Table 2). However, the absolute and relative distribution of dry weight between reproductive and vegetative tissue was altered drastically in the shoot (Table 2). Seedheads from plants that had been cold treated for 8 weeks and from unvernalized controls

Table 1. The effect of plant age at harvest on the time from planting to flowering, seedhead formation, dry weight of seedheads, total shoot dry weight, and the ratio of seedhead dry weight to vegetative shoot dry weight of unvernalized jointed goatgrass grown in the greenhouse^a.

Age at harvest	Time to flowering		Dry wt per seedhead	Total shoot dry wt	Seedhead dry wt/ vegetative shoot dry wt
— (d	lays)——	(no.)	(į	g) 	(g/g)
272	197 ± 2	9.4 ± 2.4	0.11 ± 0.01	31.39 ± 3.20	0.06 ± 0.03
286	203 ± 5	23.8 ± 5.1	0.10 ± 0.01	52.79 ± 2.40	0.06 ± 0.02
300	216 ± 6	24.2 ± 5.2	0.11 ± 0.01	50.71 ± 3.10	0.06 ± 0.01
314	222 ± 7	42.7 ± 6.1	0.10 ± 0.01	56.64 ± 2.10	0.09 ± 0.01
328	219 ± 4	46.7 ± 6.4	0.13 ± 0.01	45.49 ± 2.30	0.17 ± 0.03

^aValues are means ± SE (N = 20).

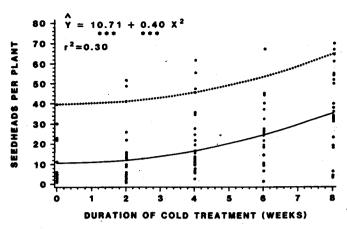


Figure 2. The effect of the duration of vernalization on the number of seedheads per plant of jointed goatgrass 272 days after transplanting in the greenhouse. The best fitting regression equation and 95% confidence interval are presented for the pooled data. The stars indicate that the intercept and coefficients were significantly different from zero (P<0.0001).

contributed 59.8 and 5.6% of the total dry-matter accumulation, respectively (Table 2). The relationship between the ratio of reproductive to vegetative tissue and the duration of vernalization was modeled best by a quadratic equation $(P = 0.0001, r^2 = 0.35)$. Because total shoot dry weight did not change for vernalized plants, these ratios can be compared directly (Table 2).

As unvernalized plants aged, their total shoot dry weight increased in a linear fashion (P = 0.0001, $r^2 = 0.13$) (Table 1). The ratio of reproductive to vegetative tissues of unvernalized plants was altered less by plant age (Table 1) than by duration

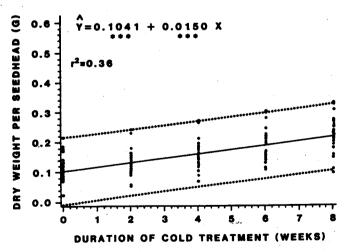


Figure 3. The effect of the duration of vernalization on the dry weight per seedhead of jointed goatgrass 272 days after transplanting in the greenhouse. The best fitting regression equation and 95% confidence interval are presented for the pooled data. The stars indicate that the intercept and coefficients were significantly different from zero ($P \le 0.0001$).

Table 2. The effect of various periods of vernalization at 3 C on the shoot dry weights and the ratios of seedhead dry weight to vegetative shoot dry weight of jointed goatgrass 272 days after transfer from the cold treatment to a greenhouse^a.

Duration of vernalization	Age at harvest	Total shoot dry wt	Seedhead dry wt/ vegetative shoot dry wt
(weeks)	(days)	(g)	(g/g)
0	272	31.37 ± 3.21	0.06 ± 0.03
2	286	36.28 ± 2.92	0.05 ± 0.01
4	300	35.21 ± 2.46	0.14 ± 0.03
6	314	31.76 ± 2.63	0.30 ± 0.05
8	328	30.79 ± 1.53	0.60 ± 0.06

 $^{^{}a}$ Values are means \pm SE (N = 20).

of vernalization for unvernalized plants (Table 2). As unvernalized plants aged, they distributed more dry matter to their seedheads. The relationship between seedhead dry weight and age of unvernalized plants was described best by a quadratic equation (P = 0.0001, r² = 0.18). The oldest, unvernalized plants produced 7.7 g of seedhead material per plant, whereas plants that were chilled for 8 weeks and were the same chronological age produced 18.4 g.

Duration of vernalization of seedlings. As Silsbury (32) pointed out, determination of the vernalization response using imbibed seed assumes that the seed response and that of the yegetative plant are similar. This appeared to be the case for jointed goatgrass. Seed that were vernalized at 3 ± 2 C in a coldroom for 8 weeks and seedlings that were chilled outdoors for 8 weeks matured at the same time after transfer to the greenhouse (Figures 1 and 5). All of the plants that were vernalized outdoors had flowered by the end of the experiment. The population of unvernalized plants started in August took between 160 to 270 days in 1981 and 180 to 250 days in 1982 to begin flowering (Figure 4). Thus, jointed goatgrass does not have an obligate requirement for vernalization in order to flower.

The time needed for jointed goatgrass to flower, once plants resumed growth after being brought into the greenhouse, depended upon the duration of chilling outdoors (Figure 5). As was observed for imbibed seed, increasing periods of cold treatment later reduced the time needed for established plants to mature and flower. However, vernalization of seedlings for more than 120 days did not further decrease the time required for flowering. This response was similar to that of 'Petkus' rye (31). Assuming that further vernalization would be without additional effect on the days to flower and that devernalization in the spring is minimal prior to floral induction, fall-germinated jointed goatgrass would need about 90 days to flower following resumption of growth in the spring. This interval of time is long enough to ensure that jointed goatgrass would not experience damaging frost during floral development (18), even in North Dakota.

Winters are more severe and longer in duration in North Dakota than in eastern Colorado, the site of origin for this

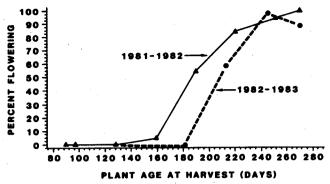


Figure 4. The percent of unvernalized plants of jointed goatgrass of various ages that flowered in the greenhouse 272 days after being started in August (N = 20). All plants brought indoors after various periods of cold treatment outdoors had flowered at harvest.

selection of jointed goatgrass. Consequently, if this experiment were conducted in Colorado, it might change the time that would be needed for a maximum response to vernalization.

Season of establishment of seedlings. The results of this field experiment verified and extended the observations that were made in the first two experiments. Plants started in August through February or March were vernalized either as established seedlings or imbibed seed and flowered in the following summer (Figure 6). As the planting date advanced from March to May of 1981 and February to May of 1982, the proportion of flowering plants decreased. The winter of 1981 to 1982 was considerably colder and of longer duration than the winter of 1982 to 1983. The maximum winter temperatures were -35 and -23 C, respectively.

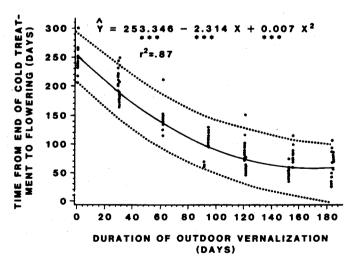


Figure 5. The effect of duration of cold treatment outdoors on the time needed to flower following transfer of jointed goatgrass into the greenhouse. The best fitting regression equation and 95% confidence interval are presented for the pooled data. The stars indicate that the intercept and coefficients were significantly different from zero ($P \le 0.0001$).

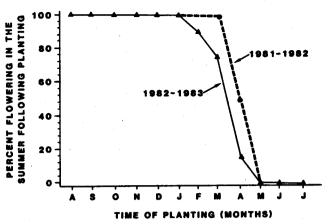


Figure 6. The effect of planting date on the proportion of jointed goatgrass plants that flowered in the summer after seeding (N = 20).

Consequently, a higher proportion of the plants started in March and April flowered in 1982 than in 1983. Apparently, the spring period of cold was insufficient for adequate vernalization of the later plantings. All treatments that were started in April to July became established during the summer, but none planted in May, June, or July of 1981 or 1982 flowered in the year that they were planted outdoors. However, the few plants that survived the subsequent winter following midsummer planting flowered during the following spring.

The goatgrass plants that were planted and became established from August to November of 1981 and from August to October of 1982 did not die over winter (Table 3). The August to September plantings tillered well in the fall of both years. Jointed goatgrass, which was seeded outdoors from December to March of both years, either failed to emerge or emerged erratically in the following spring. When few plants ($N \le 3$) became established for a planting date, the data were not presented.

Plants that were started in the fall took less time to flower after resuming growth in the spring than those started in the spring (Table 3). Plants that were started in December to April and flowered required more time to mature than plants started in the fall (89.9 compared to 132.5 days in 1982, and 60.8 compared to 95.3 days in 1983). As noted earlier, this time interval is long enough to minimize the chance of damaging exposure to frost during floral development. The time needed to flower in the field was somewhat longer than expected based on results of the other greenhouse experiments.

Plants that were started in the fall and winter were less variable in their flowering behavior. Vernalization may be a way of synchronizing the plant's life cycle with climate (30). Synchronization of plant life cycles may be needed in environments where rainfall is sporadic in the fall and leads to erratic germination. The flowering of musk thistle (Carduus nutans L. # CRUNU) involved a vernalization requirement which later synchronized the flowering of seedlings that germinated at different times during the autumn

Table 3. The effect of date of planting in the field on the time from regrowth in the spring or emergence to flowering of jointed goatgrass in the following summer.

Time of planting ^a	Sample size	Time from spring growth to flowering	Standard error	Coefficient of variation	Range
(date)	(no.)	(days)			(days)
Replicate 1					
8/ 4/81 R	17	33.9	1.5	17.6	16
9/12/81 R	20	37.2	0.9	10.8	16
10/13/81 R	18	41.9	0.7	6.8	9
11/12/81 R	9	52.8	2.5	13.9	17
12/12/81 E	5	101.0	16.7	36.9	85
1/12/82 E	12	89.9	9.1	34.9	106
3/ 9/82 E	14	100.6	5.2	19.3	78
4/ 7/82 E	4	132.5	37.8	57.1	145
Replicate 2		-	-	1	
8/ 4/82 R	17	47.3	0.9	7.5	12
9/ 2/82 R	17	45.7	0.8	7.2	12
10/ 5/82 R	15	45.5	1.0	8.3	12
1/ 6/83 E	11	70.9	5.9	27.5	63
2/ 3/83 E	17	60.8	0.7	4.6	9
3/ 3/83 E	13	68.2	3.6	19.2	42

 $^{^{}a}R$ = Regrowth in the spring of plants that were established in the fall, E = Plants emerging in the spring.

or fall of the previous year (25). Synchronization of flowering was observed in this study (Table 3), and the flowering biology of jointed goatgrass demonstrates that its life cycle is geared to seasonal changes in the environment like other winter annuals (21).

If jointed goatgrass seed, which were shed in the fall, did not become imbibed, they would not be vernalized. Unvernalized jointed goatgrass seed that germinate in the spring are unlikely to produce plants that set seed in the year of establishment. Unvernalized seed germinating in March or April, when conditions first permit seedling establishment, would require approximately 7 to 8 months to begin flowering in September to October in the Central Great Plains. Spring germination of jointed goatgrass has been observed in the field in Colorado. If the land were summer fallowed and tilled repeatedly, unvernalized seedlings would not have a chance to mature prior to winter. Likewise, seedbed preparation in August and September following winter wheat harvest would kill established, unvernalized plants prior to flowering. Thus, plants germinating in the spring from unvernalized seed are unlikely to form seed in the same growing season. In contrast, small plants overwintering as seedlings or vernalized as imbibed seed and germinating in the spring would have adequate time to flower, mature, and shed seed prior to winter wheat harvest.

Vernalization requirements for flowering may also be an adaptation to dry summer habitats (2). Thus, vernalization of the winter annual [Alyssum alyssoides (L.) Natth. # AYSAC] is needed for this species to complete its life cycle prior to the onset of summer drought. Nonvernalized plants are less likely to survive summer drought and flower later. Many of the winter annual weeds of winter wheat complete their life cycles either prior to or with winter wheat (8, 14).

Jointed goatgrass is distributed from Texas to Washington in the United States (8). It is likely that vernalization requirements for flowering differ between selections from different parts of this range. Vernalization requirements may even control the potential distribution of different ecotypes of this species, as it does for slender oat in Australia (27). This study establishes that jointed goatgrass can grow and reproduce in eastern North Dakota. However, there are many more rotational crops and herbicides that can be used to control jointed goatgrass in the Northern Great Plains than in much of the winter wheat-growing area of the Central and Southern Great Plains.

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