Stability of Nonflowering Orchardgrass

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ABSTRACT

Orchardgrass (*Dactylis glomerata* L.) is a valuable pasture species in much of temperate humid North America. However, profuse and early flowering in spring creates management problems for graziers and reduces intake of livestock in a management-intensive rotational grazing system. The objectives of this study were to estimate environmental stability, genotypic variability, and frequency of nonflowering and sparse-flowering plants in two sparse-flowering orchardgrass populations. Seven cultivars and 299 half-sib families were evaluated for 2 yr at five locations between 42° and 47° N latitude. Sparse-flowering populations WO-SF-B and WO-SF-C were later in maturity, produced fewer panicles per plant, and had higher frequencies of sparse-flowering and nonflowering plants than the cultivars. Plants had varying levels of expression of the nonflowering trait, ranging from slightly sensitive (sparse flowering in one year) to highly sensitive (stable nonflowering across years), with highly sensitive plants found only within populations WO-SF-B and WO-SF-C. The nonflowering trait of orchardgrass appears to be controlled by floral-regulation genes that are turned off by short-day temperatures below a critical threshold. Such a threshold appears to exist for all orchardgrass plants, but is increased in those plants expressing the nonflowering trait.

Orchardgrass is a valuable pasture species in much of temperate humid North America. However, profuse and early flowering in spring creates management problems for graziers and reduces intake of livestock in a management intensive rotational grazing system (Peterson et al., 1958). Among many graziers, orchardgrass has developed a reputation as an undesirable pasture species, reducing interest in the species and contributing to a lack of demand and a resulting oversupply of orchardgrass seed. A proliferation of relatively ordinary cultivars developed in the late 20th century, with few special or novel characteristics, has contributed to this reduced demand and oversupply by failing to recognize the traits of interest to graziers (Casler et al., 2001).

Late heading cultivars provide one potential solution to this problem, allowing greater flexibility during the early-spring grazing rotation. However, late heading is not a panacea, because some late-heading cultivars can have reduced net herbage accumulation under rotational grazing (Casler et al., 2001) or reduced survival (Casler et al., 2000). Because reduced intake from spring grazing of orchardgrass is related to heading, nonflowering or sparse-flowering germplasm might provide an alternative solution to this problem (Peterson et al., 1958). These authors further suggested that nonflowering strains of forage grasses would simplify management of grass-legume mixtures and have a more uniform distribution of dry matter production throughout the growing season.

Orchardgrass largely behaves as a short-day–long-day plant that requires prolonged exposure to short days for floral induction (primary induction) followed by long days for floral initiation (secondary induction) and development (Calder, 1964; Gardner and Loomis, 1953; Heide, 1987). Genotypes vary widely in photoperiod requirement for floral initiation, from 8 h for Mediterranean germplasm to 12 h or greater for northern European germplasm. Exposure to cold temperatures is not specifically required for flowering, but extreme cold can result in floral induction under continuous light (Blondon, 1985). Heide (1987) suggested that low temperatures may render orchardgrass plants indifferent to daylength, resulting in a typical vernalization response and normal flowering. Furthermore, short-day induction becomes less effective as the temperature approaches freezing (Heide, 1987).

Hovin et al. (1966) developed two orchardgrass populations that had normal panicle and seed production in eastern Washington, but severely reduced panicle production in Pennsylvania and Vermont (Berg et al., 1981). Pennsylvania has lower winter temperatures than the Washington location, resulting in a shorter growing season. Berg et al. (1981) speculated that plants growing in Pennsylvania have a longer winter dormancy than those growing in Washington, restricting their physiological activity during the short-day induction period, severely reducing panicle production. This trait appears to be under the control of a fairly large number of loci (Berg et al., 1981; Hovin et al., 1966).

The use of nonflowering or sparse-flowering orchardgrass cultivars will require careful identification of genotypes that will flower reliably in a designated seed-production environment and will retain their nonflowering or sparse-flowering trait in forage-production environments (Peterson et al., 1958). Orchardgrass cultivars are a highly heterogeneous mixture of genotypes, containing large amounts of genetic variability, some of which can be observed among segregating progeny and some of which is locked up in its autotetraploid genome. Both the frequency and stability of nonflowering and sparse-flowering plants within a cultivar will determine the economic success and/or value of a nonflowering or sparse-flowering orchardgrass cultivar.

The objectives of this study were (i) to evaluate the environmental stability of two sparse-flowering orchard-

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grass populations across several locations, (ii) to determine the level of genotypic variability for the nonflowering and sparse-flowering traits in these populations, and (iii) to quantify the frequency of stable nonflowering and sparse-flowering plants in these populations.

MATERIALS AND METHODS

The germplasm for this study derived from two sparse-flowering orchardgrass populations first described by Hovin et al. (1966) as Syn B and Syn C (since renamed WO-SF-B and WO-SF-C, respectively). Seed produced in 1966 at Prosser, WA, was maintained at −3°C and supplied by C.C. Berg (deceased) of the U.S. Pasture and Watershed Research Lab at University Park, PA.

Plants of each population were raised in a greenhouse and transplanted to the field at Corvallis, OR, in October 1993 as 12-wk-old seedlings. The soil was a Woodburn silt loam (fine-silty, mixed mesic, Aquultic Agrixerolls). Plants were spaced on 1.0-m centers in separate crossing blocks for each population, isolated from other orchardgrass by a minimum of 100 m. Weeds were controlled by a combination of mechanical and chemical methods. In spring 1994, plants were fertilized with 56 kg N ha^{-1}. Seed was harvested on 110 of 680 plants from WO-SF-B and 189 of 1000 plants from WO-SF-C in July 1994. Harvested plants were selected for vigor, a healthy appearance, and a high frequency of panicle production relative to other plants of the population. Panicles were harvested from individual plants into paper bags, hand threshed after air drying, and conditioned using a combination of screens and air separation.

Seed of each half-sib (open-pollinated) family and seven check cultivars (AC Nordic, Albert, Comet, Dawn, Hallmark, Justus, and Pennlate) were distributed to the five locations described in Table 1. Ten seedlings of each family and 30 seedlings of each cultivar were raised in a greenhouse and transplanted to the field at each location at approximately 15 wk of age. Field studies were established in September 1998 at Corvallis or May 1998 for the other locations. The experimental design was a randomized complete block with two replicates. Plots consisted of a linear row of five seedlings spaced 30 cm apart with adjacent rows 0.9 m apart. The seven cultivars were repeated three times within each replicate. The experimental areas at Arlington and Ashland were overseeded with a mixture of fine fescues [*Festuca rubra* L. subsp. *rubra* Gaudin, *F. rubra* L. subsp. *commutata* (Thuill.) Nyman, and *F. trachyphylla* (Hackel) Krajina] seeded at a rate of 182 kg ha^{-1}. The experimental areas at Charlottetown and Ithaca were overseeded with a small-leaf white clover (*Trifolium repens* L.) seeded at a rate of 4 kg ha^{-1}. Plants were mowed two or three times during the establishment year and fertilized with 56 kg N ha^{-1}.

Plants were fertilized with 56 kg N ha^{-1} in early spring of 1999 and 2000. Data were collected on each plant when plants of the latest maturing cultivars had reached a minimum of the panicles-emerged growth stage. Relative maturity was rated on one day for all plants using the following scale: 1 = vegetative, 2 = panicles in the boot, 3 = panicles emerging, 4 = panicles fully emerged, 5 = peduncles fully elongated, 6 = initial anthesis, 7 = full anthesis, 8 = postanthesis, and 9 = seed ripening. The number of panicles was counted on each plant.

Four variables were analyzed by analysis of variance: relative maturity of plants with at least one panicle at the time of scoring (i.e., nonheaded plants were ignored), number of panicles per plant, percentage of sparse-flowering plants per plot (1–10 panicles per plant) and percentage of nonflowering plants per plot (no panicles). Two levels of ANOVA were applied to these data. First, a combined ANOVA was conducted over years and locations using the split-plot-in-time model (Steel et al., 1997). Second, due to genotype × environment interactions, data from each location and year were analyzed separately. Locations and years were considered to be fixed effects, while families, cultivars, and replicates were considered to be random effects. All variables were analyzed on a plot-mean basis. Means for populations WO-SF-B and WO-SF-C and the cultivars were compared by contrasts.

Genotypic correlation coefficients between the four variables were computed according to Mode and Robinson (1959). Cluster analysis, based on Euclidean distances, was used to determine the relationships among locations for each of the four variables. Principal components analysis of the means over locations and years for the four variables was used to describe phenotypic differences between the two sparse-flowering populations and the cultivars.

Finally, stable nonflowering plants (SNFP) and stable sparse-flowering plants (SSFP) were defined as those plants that had the required characteristic in both 1999 and 2000. The frequencies of SNFP and SSFP were analyzed by chi-square to test frequency differences among locations, between populations, and between populations and cultivars. The location-mean frequencies of SNFP and SSFP were regressed on latitude and mean temperature of the coldest month for the experimental period of May 1998 to July 2000. Daily mean, high, and low temperatures were recorded at each of the five locations throughout the experimental period. Regression models were chosen based on visual inspection of scatterplots and model fitting criteria (Ratkowsky, 1990).

RESULTS AND DISCUSSION

The two sparse-flowering orchardgrass populations were later in maturity than the cultivars at all locations and years (Table 2). This relationship held true regardless of the maturity stage at which data were collected, which varied somewhat across locations and years. Furthermore, both sparse-flowering populations were later than the latest maturing cultivar in the study, AC Nordic, at all locations and years. On average, the difference between the sparse-flowering populations and cultivars represents the difference between preanthesis and full anthesis, a difference of approximately 4 to 8 d, depend-

Table 1. Ecogeographic information for the five locations used to evaluate two sparse-flowering orchardgrass populations.

Location	Latitude	Longitude	Soil type	Mean winter temperature†
				°C
Ashland, WI	46° 35′ N	90° 58′ W	Portwing silt loam (fine, mixed, superactive, frigid Oxyaquic Glossudalfs)	−2.5
Charlottetown, PEI	46° 21′ N	63° 9′ W	Charlottetown fine sandy loam	−4.1
Corvallis, OR	44° 34′ N	123° 16′ W	Woodburn silt loam (fine-silty, mixed, mesic Typic Argiudolls)	6.0
Arlington, WI	43° 20′ N	89° 23′ W	Plano silt loam (fine-silty, mixed, mesic, superactive Aquultic Argixerolls)	−3.3
Ithaca, NY	42° 27′ N	76° 31′ W	Williamson silt loam (coarse-silty, mixed, active, mesic Typic Fragiudepts)	−1.9

† Mean daily temperature from 1 November to 31 Mar. 1971 through 2000.

Table 2. Mean maturity scores of plants with at least one panicle for two sparse-flowering orchardgrass populations and seven orchardgrass cultivars evaluated for 2 years at five locations.

	Ashland, WI		Charlottetown, PEI		Corvallis, OR		Arlington, WI		Ithaca, NY		
Population/Comparison	1999	2000	1999	2000	1999	2000	1999	2000	1999	2000	Mean
						Score†					
WO-SF-B	6.2	6.2	4.8	5.1	5.5	4.2	6.8	6.0	5.7	3.4	5.4
WO-SF-C	6.0	6.2	4.9	5.1	5.3	4.1	6.9	5.8	6.0	3.3	5.4
Cultivars	6.7	6.8	6.5	6.5	6.8	6.2	8.4	6.7	7.3	5.7	6.8
PSD‡	0.5	0.3	0.4	0.2	0.5	0.9	0.5	0.3	0.3	0.8	0.3
						P values					
B vs. cultivars	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
C vs. cultivars	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
B vs. C	0.02	0.05	0.27	0.54	<0.01	0.07	0.47	<0.01	<0.01	0.01	0.87

† Maturity score: 1 = vegetative, 2 = panicles in the boot, 3 = panicles emerging, 4 = panicles fully emerged, 5 = peduncles fully elongated, 6 = initial anthesis, 7 = full anthesis, 8 = postanthesis, and 9 = seed ripening.
‡ Phenotypic standard deviation among cultivar means.

ing on environmental conditions. The two sparse-flowering populations differed slightly in maturity from each other for some locations and years, frequently changing their ranking, but were identical in maturity averaged over all locations and years.

The two sparse-flowering populations produced fewer panicles per plant than the cultivars in all locations and years (Table 3). This occurred over a range of average panicle production from 14 to 110 panicles plant^{-1} for the cultivars. Cultivars varied substantially in panicle number, but means of the two sparse-flowering populations rarely overlapped with the distribution of panicle number for the cultivars (data not shown). On average, WO-SF-B produced 37% fewer panicles and WO-SF-C produced 49% fewer panicles than the cultivars. WO-SF-C produced fewer panicles than WO-SF-B at seven of the 10 location-years, averaging 20% fewer panicles than WO-SF-B averaged across all environments. Averaged over years, the smallest relative differences between the two sparse-flowering populations and the cultivars occurred at Corvallis where WO-SF-B was 12% lower and WO-SF-C was 35% lower than the cultivars and Ithaca where WO-SF-B was 18% lower and WO-SF-C was 35% lower than the cultivars. These two locations historically have the highest mean winter temperatures of the five locations in this study (Table 1). Exposure to extreme cold (−20°C without snow cover) can damage floral primordia, reducing panicle production (Niemeläinen, 1990).

Population WO-SF-C was consistently higher than WO-SF-B in frequency of sparse-flowering plants, with a significant difference at eight of 10 location-years and averaging 27% higher than WO-SF-B (Table 4). Population WO-SF-C was also consistently higher than the mean of the cultivars in frequency of sparse-flowering plants, with a significant difference at six of 10 location-years ($P = 0.09$ for two others) and averaging 109% higher than the cultivars. Population WO-SF-B was not consistently different from the cultivars in frequency of sparse-flowering plants. For WO-SF-B and WO-SF-C, the frequency of sparse-flowering plants was relatively consistent between years within locations, but highly variable among locations. The two Wisconsin locations had the highest frequencies of sparse-flowering plants.

Differences among WO-SF-B, WO-SF-C, and the cultivars for the frequency of nonflowering plants were not consistently significant across locations and years (Table 5). However, the ranking of these three groups was nearly constant across locations and years—WO-SF-C > WO-SF-B > cultivars—resulting in significant differences among all three groups averaged over locations and years. Populations WO-SF-C and WO-SF-B had 233 and 192% more nonflowering plants, respectively, than the mean of the cultivars, while WO-SF-C was only 14% higher than WO-SF-B in frequency of nonflowering plants. The frequency of nonflowering plants was highly unstable across both locations and years.

The four traits above were organized into principal components, the first two of which accounted for 89% of the variability among family and cultivar means. The first component was described by early maturity, many panicles per plant, and few non or sparse-flowering

Table 3. Mean number of panicles per plant for two sparse-flowering orchardgrass populations and seven orchardgrass cultivars evaluated for 2 yr at five locations.

	Ashland, WI		Charlottetown, PEI		Corvallis, OR		Arlington, WI		Ithaca, NY		
Population/Comparison	1999	2000	1999	2000	1999	2000	1999	2000	1999	2000	Mean
						Panicles plant^{-1}					
WO-SF-B	17.5	7.6	11.5	60.9	55.0	77.3	14.1	35.5	42.8	69.6	39.2
WO-SF-C	12.1	7.2	12.2	58.2	39.7	57.4	10.4	29.4	38.8	47.2	31.3
Cultivar mean	20.5	13.9	69.4	109.5	61.5	88.6	47.9	70.1	52.6	83.7	61.8
PSD†	5.0	4.9	24.8	11.9	13.4	16.4	19.6	11.5	5.5	4.8	3.6
						P values					
B vs. cultivars	<0.01	<0.01	<0.01	<0.01	0.02	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
C vs. cultivars	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
B vs. C	<0.01	0.37	0.46	0.07	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01

† Phenotypic standard deviation among cultivar means.

Table 4. Mean frequency of sparse-flowering plants (1 to 10 panicles per plant) within two sparse-flowering orchardgrass populations and seven orchardgrass cultivars evaluated for 2 yr at five locations.

	Ashland, WI		Charlottetown, PEI		Corvallis, OR		Arlington, WI		Ithaca, NY		
Population/Comparison	1999	2000	1999	2000	1999	2000	1999	2000	1999	2000	Mean
WO-SF-B	0.309	0.422	0.062	0.109	0.100	0.071	0.349	0.157	0.063	0.047	0.169
WO-SF-C	0.364	0.425	0.057	0.148	0.156	0.130	0.423	0.236	0.080	0.128	0.215
Cultivar mean	0.237	0.387	0.055	0.006	0.038	0.038	0.172	0.040	0.024	0.030	0.103
PSD†	0.140	0.057	0.044	0.015	0.045	0.013	0.112	0.036	0.016	0.044	0.027
						P values					
B vs. cultivars	0.37	0.63	0.82	0.10	0.18	0.42	0.02	0.04	0.23	0.65	0.23
C vs. cultivars	0.09	0.61	0.96	0.02	0.01	0.03	<0.01	<0.01	0.09	<0.01	0.04
B vs. C	<0.01	0.85	0.37	<0.01	<0.01	<0.01	<0.01	<0.01	0.01	<0.01	<0.01

† Phenotypic standard deviation among cultivar means.

plants and accounted for 69% of the variability. This component separated the seven cultivars from all but one of the 299 half-sib families of WO-SF-B and WO-SF-C (Fig. 1). The second component was largely described by a high frequency of sparse-flowering plants and accounted for 20% of the variability. The second component resulted in a small degree of separation between WO-SF-B and WO-SF-C, largely identifying some families of WO-SF-C that had a high frequency of sparse-flowering plants. While populations WO-SF-B and WO-SF-C were not very distinct from each other, they were clearly distinct from the seven cultivars included in this study.

Genetic variability was significant and substantial within both WO-SF-B and WO-SF-C, although of a similar magnitude for both populations (Table 6). Narrow-sense heritability was moderate for all four traits, indicating that selection for a higher frequency of sparse- and/or nonflowering plants should result in greater separation of these populations from typical cultivated orchardgrass germplasm. The frequencies of sparse-flowering and nonflowering plants were positively correlated with each other and negatively correlated with maturity and panicles per plant (Table 7). Further selection for a higher frequency of sparse-flowering or nonflowering plants will probably result in later maturing germplasm with a lower frequency of panicles per plant. Consistent negative genetic correlation coefficients of the frequency of sparse- and nonflowering plants with maturity and panicle number across populations, locations, and years (data not shown) suggest that this would occur regardless of the selection environment, provided that there is expression of the sparse- or nonflowring trait.

The frequency of SSFP and SNFP were highly variable across locations ($P < 0.0001$ from chi-square tests) for both populations (Table 8). The two populations reacted similarly across locations. The exponential regressions of SSFP and SNFP on mean temperature of the coldest month were both significant (Fig. 2). Both SSFP and SNFP declined asymptotically with increasing temperature of the coldest month. Latitude, or daylength, could not explain the variability among locations for SSFP or SNFP. These regressions suggest that there is probably a threshold temperature above which floral primordia and panicle production of orchardgrass plants is unaffected. However, when winter temperatures fall below this temperature for a sustained period of time, panicle production is significantly impaired. This reduction in panicle number increases as temperature is reduced below this threshold level, which appears to be approximately −7 to −5°C on a monthly-mean basis.

All stable sparse-flowering plants and stable nonflowering plants (those plants that consistently expressed this trait over 2 yr) were identified from within WO-SF-B and WO-SF-C; none of these plants occurred within the seven cultivars. The cultivars also appeared to be sensitive to winter temperature, but with a much lower threshold temperature than WO-SF-B and WO-SF-C. For the cultivars, the highest frequencies of sparse-flowering plus nonflowering plants (Tables 4 and 5) and the lowest number of panicles per plant (Table 3) occurred in both years at Ashland, the coldest of the five locations. Considering panicles per plant and the sum of sparse-flowering and nonflowering plants as two measures of sensitivity to cold winter temperatures, floral primordia of the cultivars appeared to be heavily damaged by cold only at Ashland, suggesting a monthly mean threshold temperature for the cultivars somewhere between −12 and −8°C. These estimates are higher than the −20°C used by Niemeläinen (1990), who demon-

Table 5. Mean frequency of nonflowering plants within two sparse-flowering orchardgrass populations and seven orchardgrass cultivars evaluated for 2 yr at five locations.

	Ashland, WI		Charlottetown, PEI		Corvallis, OR		Arlington, WI		Ithaca, NY		
Population/Comparison	1999	2000	1999	2000	1999	2000	1999	2000	1999	2000	Mean
WO-SF-B	0.113	0.340	0.704	0.002	0.022	0.012	0.278	0.061	0.016	0.020	0.157
WO-SF-C	0.204	0.355	0.718	0.002	0.042	0.035	0.295	0.085	0.012	0.041	0.179
Cultivar mean	0.063	0.174	0.182	0.000	0.024	0.005	0.025	0.052	0.000	0.013	0.054
PSD†	0.051	0.165	0.087	0.000	0.032	0.013	0.033	0.092	0.000	0.023	0.034
						P values					
B vs. cultivars	0.41	0.04	<0.01	0.70	0.94	0.73	<0.01	0.82	0.27	0.77	0.03
C vs. cultivars	0.02	0.02	<0.01	0.66	0.46	0.14	<0.01	0.38	0.41	0.26	0.01
B vs. C	<0.01	0.33	0.30	0.77	<0.01	<0.01	0.24	<0.01	0.15	<0.01	0.02

† Phenotypic standard deviation among cultivar means.

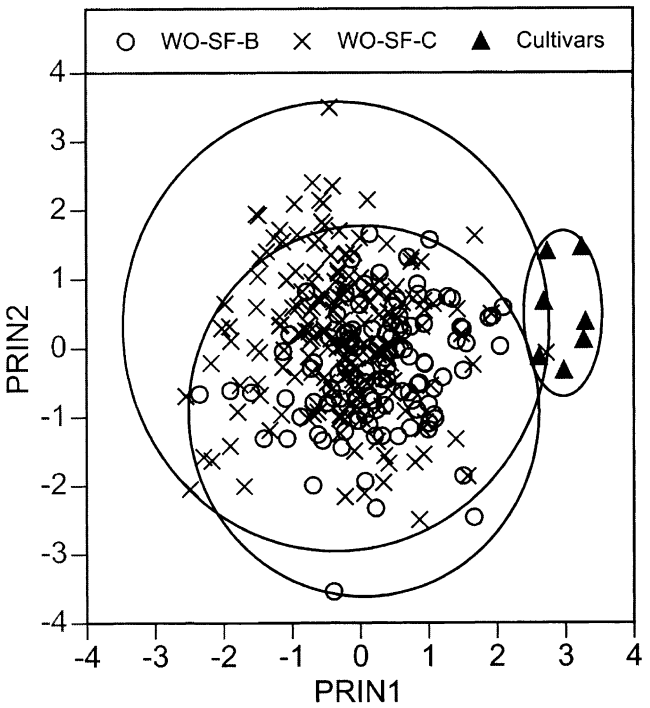

Fig. 1. Scatterplot of the first two principal components for 299 orchardgrass half-sib families and seven orchardgrass cultivars evaluated for maturity, panicle number, sparse-flowering plants, and nonflowering plants.

strated the effect of cold temperatures without snow cover on panicle production of orchardgrass.

Differential winter threshold temperatures for the sparse-flowering populations compared with the cultivars suggests genetic variation in temperature regulation of flowering in orchardgrass. This may occur as a result of differential freezing tolerance—some genotypes have floral primordia that are more sensitive to freezing temperatures. Alternatively, this genetic variability may result from differential inductive requirements. Exposure to a certain number of chilling hours is required for the normal vernalization response in extreme perennials such as orchardgrass (Canode et al., 1972; Cooper and Calder, 1964), but as temperatures approach freezing, short-day induction becomes ineffective (Heide, 1987). Furthermore, these explanations are not mutually exclusive, potentially complicating the genetic control of flowering in orchardgrass.

SUMMARY AND CONCLUSIONS

Flowering in grasses is regulated by three families of genes that interact with the environment and with each other in a complex pathway. These three gene families regulate vernalization response, photoperiod response, and earliness of heading (Takahashi and Yasuda, 1971). Vernalization genes are highly conserved across genomes within the Triticeae (Yan et al., 2003) and likely will be found to be of similar importance in non-Triticeae grasses such as orchardgrass. Flowering genes appear to be regulated by activators and repressors, which interact in response to environmental stimuli (Trevaskis et al., 2003). Furthermore, vernalization genes can mask the effects of genes that regulate photoperiodism and earliness simply by their profound effect on expression of flowering (Takahashi and Yasuda, 1971).

This study demonstrated that the frequencies of sparse-flowering and nonflowering plants are heritable in orchardgrass, conditioned by a large amount of additive genetic variability, although the number of genes controlling this trait is unknown. The frequencies of sparse-flowering and nonflowering plants are probably not different traits but different levels of expression of the nonflowering trait. Expression of this trait is environmentally sensitive, with winter (short-day) temperatures appearing as the most likely environmental regulatory factor. The nonflowering trait in orchardgrass is likely due to floral-regulation genes that are turned off by short-day temperatures below a critical threshold. Such a threshold appears to exist for all orchardgrass plants, but is increased in those plants expressing the nonflowering trait.

Orchardgrass plants express this trait to several degrees, ranging from slightly sensitive (sparse-flowering in occasional years) to highly sensitive (stable nonflowering across years). There is likely a considerable range in short-day threshold temperature sensitivity among orchardgrass genotypes. Orchardgrass breeding populations are highly heterogeneous and the autotetraploid genome contains large amounts of cryptic variability (Lumaret, 1988). Polysomic segregation, temperature sensitivity, a range of genetic expression levels, and a high potential for genetic polymorphisms combine to create a relatively high level of phenotypic instability for the nonflowering trait.

Commercialization of the nonflowering trait in orchardgrass will require improved stability of phenotypic expression. Furthermore, the nonflowering trait must be expressed in a large range of forage production environments and routinely silenced in seed production environments. Populations WO-SF-B and WO-SF-C, as they now exist, are insufficiently stable to be commercialized as nonflowering or sparse-flowering orchard-

Table 6. Half-sib family variance component estimates (s^2_{HSF}), 95% upper and lower confidence limits for family variance component estimates, and narrow-sense heritability estimates (H) for two sparse-flowering orchardgrass populations evaluated at five locations.

	WO-SF-B				WO-SF-C			
Location	s^2_{HSF}	95%LL	95%UL	H	s^2_{HSF}	95%LL	95%UL	H
Maturity	0.101**	0.042	0.173	0.66	0.090**	0.048	0.140	0.64
Number of panicles	31.40**	5.36	63.41	0.49	34.48**	15.71	57.42	0.52
Sparse-flowering plants†	10.13**	−2.58	20.86	0.54	7.18*	−5.78	20.14	0.25
Nonflowering plants†	10.91**	−2.15	25.53	0.40	12.04**	1.23	23.73	0.41

* Mean square associated with variance component was significant at $P < 0.05$.
** Mean square associated with variance component was significant at $P < 0.01$.
† Values shown are variance components $\times 10^4$.

Table 7. Genetic correlation coefficients among four variables measured on two sparse-flowering orchardgrass populations evaluated at five locations (WO-SF-B above the diagonal and WO-SF-C below the diagonal).

	Maturity	No. of panicles per plant	Sparse-flowering plants	Nonflowering plants
Maturity		0.67 ± 0.06	−0.45 ± 0.10	−0.42 ± 0.11
Number of panicles	0.51 ± 0.09		−0.79 ± 0.05	−0.68 ± 0.08
Sparse-flowering plants	−0.41 ± 0.12	−0.65 ± 0.09		0.42 ± 0.13
Nonflowering plants	−0.39 ± 0.11	−0.64 ± 0.09	0.30 ± 0.15	

Table 8. Frequencies of stable sparse-flowering plants and stable nonflowering plants for two orchardgrass populations evaluated at five locations for 2 yr.

	Stable sparse-flowering plants			Stable nonflowering plants		
Location	WO-SF-B	WO-SF-C	Overall	WO-SF-B	WO-SF-C	Overall
Ashland	0.146	0.172	0.162	0.081	0.144	0.120
Charlottetown	0.003	0.002	0.002	0.031	0.039	0.036
Corvallis	0.025	0.048	0.040	0.002	0.007	0.005
Arlington	0.069	0.103	0.090	0.050	0.066	0.060
Ithaca	0.019	0.027	0.024	0.008	0.006	0.007
Overall	0.052	0.068	0.062	0.034	0.050	0.044

grass. Panicle production in Corvallis was adequate, suggesting that seed can be produced reliably in the major orchardgrass seed production region of the USA. However, expression of the nonflowering trait was inadequate at Ithaca and inconsistent at Charlottetown, two locations with relatively mild short-day temperatures (compared with the two Wisconsin locations). The commercial potential of this trait can be realized only after additional selection of plants that have extreme expression of the nonflowering trait (SNFP) at an eastern location, combined with adequate panicle and seed production at Corvallis or another mild-winter seed production location.

Orchardgrass clones can be propagated by somatic embryogenesis (Alexandrova and Conger, 2002), leading to the possibility of commercializing single clones or groups of clones. However, such a technology would likely be prohibitively expensive for a seed market that is characterized by excessive seed inventories and low demand for improved products (Casler et al., 2000, 2001). Nevertheless, somatic embryogenesis might be useful in the seed production phase of a commercial nonflowering orchardgrass. Pairs or groups of nonflowering clones could be propagated in seed production fields on a scale sufficiently large to allow commercial release of the first-generation hybrid or synthetic. Commercial use of the first-generation hybrid or synthetic would eliminate several generations of seed multiplication and segregation that could erode the phenotypic expression of the nonflowering trait.

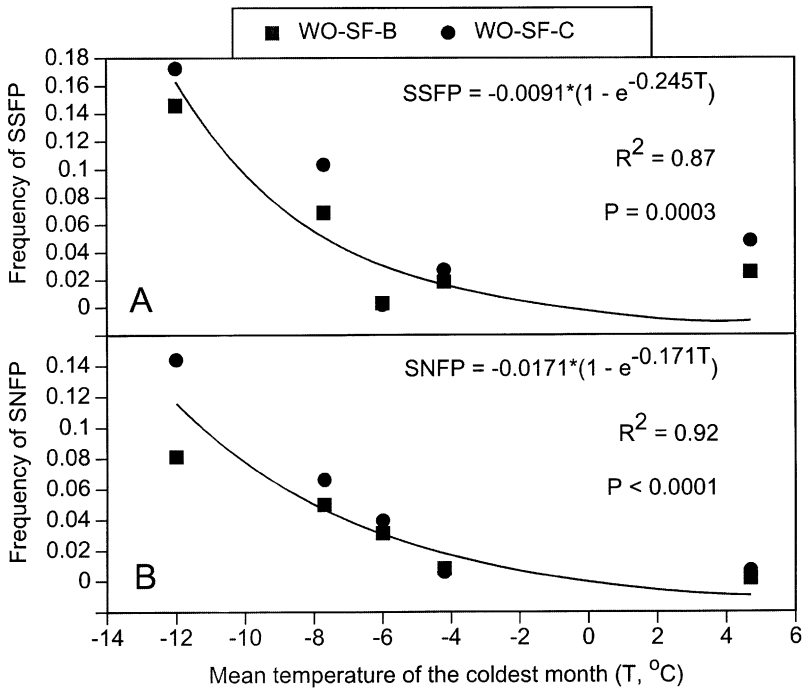

Fig. 2. Exponential regression of population and location mean frequency of (A) stable sparse-flowering plants (SSFP) or (B) stable nonflowering plants (SNFP) on mean temperature of the coldest month during the experimental period of May 1998 to July 2000. The ranking of locations for mean temperature of the coldest month, from lowest to highest, was Ashland, Arlington, Charlottetown, Ithaca, and Corvallis.

A novel trait, such as nonflowering, might be sufficiently valuable to graziers that it would warrant use of new technologies for commercial seed production. Berg et al. (1981) showed no improvement in forage quality for WO-SF-B and WO-SF-C compared to commercial orchardgrass cultivars. However, an increase in forage quality would not be necessary for nonflowering orchardgrass to have an economic impact on a management-intensive rotational grazing system. Elimination of all or most panicles during the spring flush of growth would increase management flexibility and simplify a grazing system. Orchardgrass forage could be stockpiled for a longer period of time in spring without concern over a rapid decline in quality or acceptability to grazing livestock. The results of this study suggest potential for commercial development of the nonflowering trait in orchardgrass and there are probably a sufficient number of forage-based grazing operations in temperate North America to create a commercial market for this germplasm.

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