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Original Research

Effects of Selection for Seedling Vigor on the Genetic Variation in *Leymus cinereus*☆

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ABSTRACT

Basin wildrye (*Leymus cinereus* [Scribn. & Merr. Á. Löve]) is a perennial grass native to western regions of North America. Despite its importance for rangelands, stand establishment of basin wildrye is difficult due to its poor seedling vigor. We undertook to increase the seedling vigor of the basin wildrye cultivar "Trailhead" by using selection for emergence from deep seeding depth. We carried out two cycles of selection in two select populations and included two random populations, in which no direct selection occurred. We characterized the indirection effect of the selection on biomass, seed production, and stand percentage in these populations under field conditions. We used amplified fragment length polymorphic (AFLP) markers to identify regions of the genome associated with the selection by identifying allele frequency changes between the base population and the select and random populations. The second cycle select population and the first cycle random population possessed the highest total emergence from deep seeding (60% and 59%, respectively) compared with the base population (26%). The field evaluations showed no differences in genetic variation among the base, select, and random populations for biomass, seed production, and stand percentage. On the basis of the analysis of the AFLP markers, diversity increased slightly among the random populations and decreased slightly among the select populations. In the select populations, band frequencies increased for aggcac403, actcag185, and aggcac208. The band frequencies of aggctg212 and actctc66 decreased in both random and selected cycles. The results indicate that targeted selection for trait improvement in this native grass can be successfully completed with minimal effect on population genetic diversity.

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Introduction

Disturbances to rangelands can result in loss of plant materials. This loss of plant cover exposes bare soil, increasing the soil's susceptibility to wind and water erosion; leads to invasion of sites by annual weeds that may increase the frequency of the fire cycle; and results in loss of habitat for wildlife and other ecological functions (Pyke et al., 2013). There is a need for plant materials for revegetation of these sites that rapidly establish to mitigate these losses of ecological function. In many situations, the success of revegetation is exacerbated by changing soil conditions, aridity, and competition from other undesirable species (e.g., downy brome, or cheatgrass [*Bromus tectorum* L.]) (Pyke et al., 2013). In western North America, the use of introduced plant species from Eurasia, such as crested wheatgrass (*Agropyron desertorum* [Fisch. ex Link]), was the standard revegetation approach through much of the 20th century (Asay et al., 2001). The prevailing philosophies were that these species were best adapted to establishment under harsh conditions and were coadapted with many of the invasive annual weeds. Increasing effort now focuses on the use of native North American plant materials for revegetation projects.

Unfortunately, native plants often struggle to reestablish on these disturbed sites. Disturbances are often sufficiently severe so as to permanently alter the site from its original state. These changes can affect soil profile, nutrients, hydrology, organic matter, or flora (Norton et al., 2007). One result is that plants originally native to the site may no longer be adapted to the postdisturbance conditions (Laycock, 1991). To address this lack of adaptation to disturbed sites, there has been an ongoing push to improve native plant materials through plant evaluation and selection. The objective of this selection is to improve the ability to germinate and establish more efficiently in disturbed ecosystems or under changing climates. However, selection within native plants species can be controversial (Kaye, 2001). On one hand, there is a concern that selection within native plant species might change their potential for local adaptation. On the other hand, there is concern that without selection the native plant germplasm pools may not be able to establish in the degraded landscapes. There is also concern

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about the changes plant selection will introduce into the native plant species, such that these improvements could render these species no longer native through genetic "modification" (e.g., allele frequency selection, not genetic transformation).

In this study, we undertook an evaluation of the effect of multiple cycles of selection on the basin wildrye (*Leymus cinereus* [Scribn. & Merr. Á. Löve]) cultivar "Trailhead," which is a perennial grass native to much of western North America. Basin wildrye is one of the taller native North American perennial grasses (Asay and Jensen, 1996). As such, it can provide important winter grazing for both wildlife and livestock. Additionally, its tall stature provides important cover for wildlife during the winter months (Asay and Jensen, 1996). Its natural range and habitat are primarily higher soil moistures areas, with annual precipitation ranging from about 360 to 500 mm, in the western Great Plains and Intermountain areas of the United States and Canada (Ogle et al., 2012). Basin wildrye is used for site revegetation following disturbance in its adapted region. It is susceptible to overgrazing, does not compete well with invasive weeds, and generally does not establish well due to poor germination and seedling vigor (Asay and Jensen, 1996).

Three basin wildrye cultivars are currently commercially available (Magnar, Trailhead, and Continental) and two germplasms (Tetra and Washoe) (Ogle et al., 2012). Trailhead, Tetra, and Washoe are tetraploid basin wildryes; Magnar is an octoploid; and Continental is an octoploid hybrid resulting from the cross of Magnar and chromosome-doubled Trailhead. Trailhead is currently the most widely used source of basin wildrye for revegetation projects on western rangelands. Trailhead accounted for 69% (8 029 kg) of the requested basin wildrye seed on the latest (2016) Bureau of Land Management seed request (USDI-BLM, personal communication). Trailhead originated from seed collected in Musselshell County, Montana. In evaluations of basin wildrye collected in Montana and Wyoming, Trailhead exhibited high biomass and persistence and was released without selection (USDA-NRCS, 2012).

Due to its revegetation usage and poor establishment, we used certified seed from this cultivar to examine the effect of two cycles of mass selection for emergence from deep seeding depth on the genetic variation of the resulting populations. This selection for emergence from a deep seeding has been widely used to increase seedling vigor and establishment (Johnson and Asay, 1993). Nevertheless, selection to improve a single trait often affects other traits because of genetic correlation (i.e., the extent to which multiple traits are controlled by the same genes or genetic pathways) (Lande and Arnold, 1983). The change in a specific trait in response to selection for a different trait is called *indirect selection* and can be either positive or negative. Examples of indirect selection include increasing grain yield in rice by selecting for lower numbers of tassel branches (Geraldi, 2005) and increasing water stress tolerance in grains by selecting for high stomatal conductance (Araus et al., 2002). We hypothesized that selection for emergence from deep seeding would exhibit no effect on the variation of other traits and would result in no discernible decrease in genetic variation on the basis of neutral molecular marker analysis.

Methods

Population Development

Two cycles of open-pollenation and selection within Trailhead basin wildrye resulted in the development of select and random populations. On 24 January 2005, 2 500 seeds of Trailhead were seeded at a 7.6-cm depth in sand benches (Lawrence, 1963; Asay and Johnson, 1980) in a Logan, Utah greenhouse to create the selected population. On 25 January 2005, an additional 2 500 seeds of Trailhead were seeded at a 1.3-cm depth in sand benches in the same greenhouse to create the control (randomly selected) population. Between 7 and 11 days after planting, the first 50 basin wildrye seedlings emerged from the deep seeding depth. These seedlings were kept, while the remaining unemerged seeds were discarded. All viable random seeds were allowed to germinate and emerge. After 30 days, 50 of the emerged control plants were randomly selected and maintained until the spring 2005 transplanting. These selected cycle 0 (C_0) plants became the parents of the select cycle 1 (S_1) and random cycle 1 (R_1) populations, respectively.

In spring 2005, the 50 plants from the C_0 select and random populations were transplanted to crossing blocks at a Logan, Utah field location at the Utah State University Evans Research Farm (41.698°N 111.831°W; 1 378 m above sea level; 432 mm annual precipitation; Nibley silty clay loam soil). The select and random populations were separated by 300 m perpendicular to the prevailing wind direction to minimize pollen flow between the populations. In 2006, following open pollination and seed maturation, seed was harvested from the select and random crossing blocks. The resulting S_1 and R_1 seeds were then bulked, separately.

In winter and spring 2007, the selection procedures used to develop the C_0 select and random populations in 2005 were repeated on the S_1 and R_1 seed lots. Two thousand five hundred seeds of S_1 and R_1 populations were seeded at 7.6-cm depth and at 1.3-cm depth, respectively. The same selection intensity was then used in each population to select 50 S_1 and R_1 plants to become the parents of the subsequent select cycle 2 (S_2) and random cycle 2 (R_2) generation populations.

In late spring 2007, the 50 selected S_1 and the 50 random R_1 plants were transplanted to crossing blocks at Logan, UT. The crossing blocks were again separated spatially to minimize pollen flow between the populations. In 2008, following pollination and seed maturation, S_2 and R_2 seed was harvested from the corresponding crossing blocks and bulked separately.

Direct Effects of Selection on Phenotype

In 2009 and 2012, deep seeding trials were conducted in the sand bench in the Logan, UT greenhouse to assess the direct effect of selection for rate of emergence from deep seeding on the resulting populations. In 2009, the study was seeded on 14 January in a randomized complete block with two complete blocks. Only two blocks were used in 2009 due to limited seed supply in that year. In each plot, 50 pure live seeds were planted at a 7.6-cm depth in the sand bench. The sand was irrigated as needed throughout the study to maintain a moist medium for seedling growth and development. Three populations were included in the study (C_0, S_1, and R_1). The S_2 and R_2 populations were not included in 2009 because seed was not yet available for these populations. Emerged seedlings in each plot were counted daily for 21 days following seeding.

The deep seeding evaluation was repeated and expanded in 2012 to include the S_2 and R_2 populations. Plots were seeded on 20 September following the 2009 protocol. The populations used in the 2012 evaluation were C_0, S_1, R_1, S_2, and R_2. The experimental design was a split-plot modification of randomized complete block design with four complete blocks. The split blocks corresponded to different soil mediums (100% sand, 67% sand and 33% clay, 33% sand and 67% clay, and 100% clay). The different soil mediums were used to determine if the populations differed in their emergence from different soils. Emerged seedlings in each plot were counted daily for 22 days following seeding.

At the completion of the deep seeding studies, the counts were summed to determine the total number of emerged seedlings (%) and transformed using the methods of Asay and Johnson (1980) to determine the rate of seedling emergence (seedlings $\cdot$ d^{-1}). These values were then submitted for analysis using the "lme4" package (Bates et al., 2013) of R (R Core Team, 2015). Populations, soil mediums, and their interaction were considered to be fixed effects, while year and block were considered to be random effects. Least square means and least significant differences (5%) were estimated from this analysis. Results were based on analysis across both years of the evaluation.

Indirect Effects of Selection on Phenotype

The indirect effects of selection for seedling vigor from deep seeding on biomass production, plant height, and seed production were evaluated at field sites in Box Elder and Cache Counties in Utah. The Cache site was the previously described USU Evans Farm, and the Box Elder site was the USU Blue Creek Research Farm (41.934°N 112.438°W; 1 567 m above sea level; 390 mm annual precipitation; Timpanogos silt loam soil). The experimental design at both locations was a randomized complete block with three complete blocks. Plots were dormant seeded with a Wintersteiger cone seeder (Wintersteiger AG North America, Salt Lake City, Utah) in November 2010. Each plot consisted of one row that was 2 m long. The seeding rate was one pure live seed $\cdot$ cm^{-1}, and the planting depth was 1.3 cm. Populations included the bulked seed from each maternal parent from the C_0, R_1, S_1, and S_2 populations (half-sib families). The R_2 population was included due to insufficient seed. Data were collected for biomass (kg $\cdot$ ha^{-1}), seed (kg $\cdot$ ha^{-1}), and stand (%) in summer 2012. Plot weights were converted to per-area weight based on the area taken up for each row. Biomass and seed production were determined by hand harvesting the aboveground plant material, separating the seed from the biomass, drying the seed and biomass at ambient air temperatures, and weighing the dried samples. Stand was measured using the frequency grid method of Vogel and Masters (2001) using only those squares laying on the row and repeated twice in each plot. For the statistical modeling, location, populations, their interactions, and blocks were all considered to be random effects. Data were analyzed using the "lme4" package of R, which was used to estimate variance, best unbiased linear predictors, and least significant differences (5%). The Levene test was used to compare the variance corresponding to each population.

Genotypic Evaluation

Amplified fragment length polymorphic (AFLP) DNA markers (Vos et al., 1995; Meudt and Clarke, 2007), generated on the ABI3730 (Applied Biosystems, Foster City, CA), were used to compare the genetic diversity of select and random populations to their parental Trailhead seed source. DNA was extracted from 48 plants of each of five entries: C_0, R_1, R_2, S_1, and S_2. Five selective AFLP primers (E-agg/M-cac, E-act/M-cag, E-act/M-ctc, E-agg/M-cac, E-agg/M-ctg) were genotyped to generate 866 markers following the methods described in Vos et al. (1995), except resolving banding patterns on an ABI3730 using Liz500 size standard (ThermoFisher, Waltham, MA). Duplicate DNA samples were included for 24 plants to estimate a genotyping error rate, and band scoring used Genographer v1.6 (Benham, 2001). From the resulting AFLP markers, the average similarity within each population (Dice, 1945; Leonard et al., 1999), and the pairwise Φ(phi)-st genetic differences between populations (Peakall and Smouse, 2006) were estimated.

To determine if any AFLP marker allele frequencies changed upon selection, pairwise contrasts were estimated for band frequencies of markers between the selected and base populations. The data were fitted to a logit model using the glimmix procedure of SAS. The estimates, Wald statistics, and their corresponding *P* values were then processed using the multtest procedure to assess the contrasts among each of the markers and simultaneously control for errors. Error rates were controlled using the false discovery rate methods. After adjusting the *P* values, the top markers were ranked by *P* value. Additionally, to estimate genetic drift, the same types of contrasts were assessed between random and base populations.

Results

Direct Effects of Selection on Phenotype

In the deep seeding evaluation, there were differences among the populations and soils for total emergence percentage ($P_{populations} = 2 \times 10^{-13}$; $P_{soils} = 0.01$) and emergence rate ($P_{populations} = 7 \times 10^{-11}$; $P_{soils} = 0.009$). However, there were not differences among the population-by-soil interaction for total emergence percentage ($P = 0.20$) or emergence rate ($P = 0.13$). The highest total emergence and emergence rate corresponded to the 2/3 and 1/3 sand-to-clay soil mixtures (Fig. 1). Nevertheless, because of the negligible population-by-soil interactions, all results are averaged across soil types. The C_0 Trailhead population possessed the lowest total emergence (26%) and emergence rate (1.2 seedlings d^{-1}) (see Fig. 1). S_2 (total emergence = 60%; emergence rate = 3.0 seedlings d^{-1}) and R_1 (total emergence = 59%; emergence rate = 2.8 seedlings d^{-1}) possessed the highest values for both traits. S_1 and R_2 possessed intermediate values for both traits.

Indirect Effects of Selection on Phenotype

Evaluations of the biomass production, seed production, and stand establishment at the Cache and Box Elder locations allowed assessment of the effect of selection for increased seedling vigor from deep seeding on the variation corresponding to these traits in the resulting basin wildrye populations. Across the two locations, there was significant population x location interaction variation for biomass ($\sigma = 0.26$; 95% confidence interval [c.i.] $= 0 - 0.43$), seed ($\sigma = 12.25$; 95% c.i. $= 9.35 - 14.68$), and stand persistence ($\sigma = 0.06$; 95% c.i. $= 0.04 - 0.08$). However, there were no main-effect phenotypic differences among the populations, either across or within individual locations, for biomass ($P = 0.57 - 0.60$), seed production ($P = 0.29 - 0.39$), or stand persistence ($P = 0.16 - 0.29$). Overall, genetic variation was similar among the R_1, S_1, and S_2 population for biomass, seed, and stand persistence at the Cache and Box Elder locations (Table 1). The Levene tests suggested no differences among the genetic variation estimates for any trait at either location ($P = 0.36 - 0.81$).

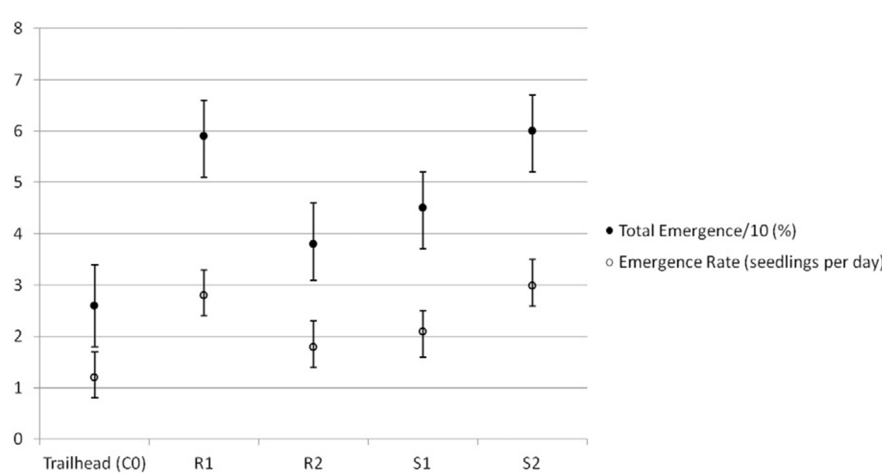

Figure 1. Mean total emergence and emergence rate values for base, random, and select populations from deep seeding depth (7.6 cm) with corresponding LSD values (error bars).

Table 1
Random (R_1) and select (S_1 and S_2) basin wildrye population standard deviation estimates (95% confidence intervals) for biomass (kg ha^{-1}), seed (kg ha^{-1}), and stand persistence (%) collected from Cache and Box Elder Counties, Utah field sites in 2012. The Levene statistic *P* value provided the test for heterogeneity of variance among the populations.

Population	Cache County, UT			Box Elder County, UT		
	Biomass	Seed	Stand persistence	Biomass	Seed	Stand persistence
R_1	0.23 (0.07, 0.35)	21.35 (13.85, 29.28)	0.03 (0, 0.09)	0.03 (0, 0.11)	0	0.09 (0.04, 0.13)
S_1	0.20 (0.05, 0.31)	19.95 (10.48, 28.57)	0	0	0	0.12 (0.09, 0.17)
S_2	0.53 (0, 1.45)	12.89 (0, 22.97)	0.07 (0, 0.12)	0.04 (0, 0.11)	1.75 (0, 3.36)	0.05 (0, 0.10)
Levene	0.53	0.74	0.73	0.77	0.36	0.81

Table 2
Diversity measures for base, random, and vigor-selected populations of *Leymus cinereus*.

Population	No.	No. bands	Polymorphism (%)	Φ-st	He	S	I
Trailhead C_0	90	355	96.42%	0.01055	0.244	0.687	0.382
R_1	46	362	93.19%	0.01016	0.246	0.681	0.382
R_2	50	356	91.22%	0.01043	0.244	0.680	0.378
S_1	44	363	92.49%	0.01042	0.248	0.685	0.382
S_2	50	361	90.18%	0.01078	0.246	0.691	0.380

No. indicates number of genotypes tested from each population; No. Bands, bands from Leonards; Polymorphism (%), from Genalex; Φ-st, from euclydian arlequin; He, from Genalex; S, from Leonards; I, (Shannon index) from Genalex.

Effects of Selection on Marker Frequency

The AFLP fingerprinting resulted in a similar number of bands (355 − 363) per population. These bands corresponded to between 90.18% (S_2) and 96.42% (C_0) polymorphic loci (Table 2). The average similarity within populations decreased for the two random populations compared with the base population (see Table 2) but increased slightly for the two select populations compared with the base population. On the basis of pairwise φ_{ST} values, changes between the random and select populations and the base population ranged from 0.7% to 1.9% (Table 3). Differences between the second cycle of randomly selected plants and the two selected cycles were also significant (see Table 3).

Compared with the base population AFLP band frequencies, both random and control exhibited 14 markers with band frequency changes (Table 4). There was a decrease in band frequencies of random or selected populations over the base population for 4 markers and an increase in 10 markers. The S_2 vs base contrast had the largest number of markers with significant differences at 10, followed by the R_1 vs base contrast at 6. Markers aggcac208, aggcac70, actcag151, and aggctg212 showed band frequency changes consistent with the selection intensity and generation. The markers aggctg212, actcag61, and aggctg64 showed frequency gains over the base in both R_1 and S_2 cycles, similar to the phenotype gains observed.

Discussion

This trait of more rapid emergence was selected because a challenge with basin wildrye when revegetating rangelands is obtaining a reliable stand. This challenge stems from slow germination and seedling elongation combined with imperfect timing of fall seed planting with rainfall events. The deep seeding selection out of Trailhead basin wildrye resulted in the development of two random (R_1 and R_2) and two select (S_1 and S_2) basin wildrye populations, and each of the four populations possessed higher total emergence and emergence rate than the base Trailhead population. Yet the various populations exhibited similar levels of variation for biomass, seed production, and stand. Thus, there was no evidence that the deep seeding selection resulted in differences among the populations for other phenotypes. By selecting specifically for seedling vigor, the selected populations have the potential to react to planting timing more efficiently while not disturbing other beneficial traits of the original Trailhead cultivar.

Table 3
Average pairwise Φ-st values among base, random, and selected populations.

Population	Trailhead C_0	R_1	R_2	S_1	S_2
Trailhead C_0	0				
Random R_1	0.0070[1]	0			
Random R_2	0.0179[1]	0^{ns}	0		
Select S_1	0.0095[1]	0^{ns}	0.0113[1]	0	
Select S_2	0.0189[1]	0.0115[1]	0.0220[1]	0^{ns}	0

[1] Significantly different at $P < 0.01$ for the pairwise contrast.

Interestingly, the highest phenotypes belonged to R_1 and S_2, the first random cycle population and the second select population, respectively. This suggested that the initial random selection from a normal seed depth was as effective as two cycles of targeted selection from the deep seeding depth. While this finding might have attributed to the effect of random drift on a finite population size (Nunney, 2002), it may also be an artifact of the seed dormancy of basin wildrye (Asay and Jensen, 1996). The random populations received no selection for seedling vigor from deep seeding, but they inadvertently received selection for decreased seed dormancy because after 30 d, not all seeds had germinated and emerged. Only those seeds that developed into a seedling in the allotted time were available for the creation of the random populations. Thus, development of the random populations also resulted in the creation of populations with decreased seed dormancy and more rapid germination. However, there was no improvement between the R_1 and R_2 populations, but rather a tendency for a decrease in seedling vigor. The selection in the S_1 and S_2 populations also resulted in selection for decreased seed dormany along with increased seedling vigor.

In contrast, the selected populations behaved as expected in a recurrent selection program aimed at increasing the frequency of beneficial additive alleles (Hallauer and Darrah, 1985). The S_1 population exhibited significantly increased total emergence and emergence rate when compared with the C_0 population. The S_2 then showed increased total emergence and emergence rate when compared with the S_1 generation, although these differences were not significant. Thus, selection for

Table 4
Amplified fragment length polymorphic (AFLP) markers with significant band frequency differences in random and/or selected populations compared with the base population.

Locus	AFLP band frequencies				
	C_0	R_1	R_2	S_1	S_2
aggcac208	0.79	0.76	0.76	0.66	0.50[1]
actcag185	0.93	0.78	0.70	0.75	0.68[1]
aggcac403	0.84	0.57	0.60	0.48[1]	0.62
actctc118	0.86	0.43[2]	0.28[2]	0.64	0.74
actcag87	0.53	0.72	0.92[1]	0.77	0.62
aggcac80	0.11	0.43[1]	0.38	0.45[1]	0.34
aggctg409	0.04	0.07	0.14	0.09	0.28[1]
aggcac70	0.14	0.11	0.18	0.30	0.42[1]
actcag151	0.17	0.35	0.34	0.39	0.46[1]
actctc66	0.02	0.28[1]	0.20	0.34[1]	0.32[1]
aggctg194	0.12	0.30	0.20	0.25	0.42[1]
actcag61	0.34	0.85[2]	0.66	0.57	0.72[1]
aggctg64	0.56	0.91[1]	0.86	0.89	0.96[1]
aggctg212	0.08	0.35[1]	0.42[1]	0.36[1]	0.50[2]

[1] Significantly different than the base frequency at $P < 0.05$.
[2] Significantly different than the base frequency at $P < 0.01$.

seedling vigor from deep seeding was effective and also highlighted the potential for simple selection to increase germination. Gains from selection result from the accumulation of alleles due to additive gene action. Gains are generally slow and accumulate over time in recurrent plant breeding prograsm. However, notable selection achievements, including increased biomass production, nutritive value, and disease resistance, are the results of ongoing selection efforts in perennial grasses (Wilkins and Humphreys, 2003). Addtionally, these gains have no effect on regions of the genome that do not underly the trait or that are not in linkage disequilibrium with genetic determinants (Bingham et al., 1994) and thus have minimal effects on underlying genetic variation.

The next objective of the study was the determination of the indirect effects of selection for seedling vigor on the level of genetic variation exhibited for other phenotypes. While there was only limited genetic variation for biomass, seed, and stand persistence, there was no evidence that selection decreased the level of genetic variation among the populations for these traits. Biomass, seed, and stand persistence can be key adaptive traits influencing basin wildrye fitness and competitiveness. If traits share common genetic determinants or are genetically linked and one of those traits is selected for (Lande and Arnold, 1983), the selection that affects one trait will also affect indirectly the other traits. In the case of selection for increased seedling vigor, these other traits were not tightly genetically linked such that specific selection for seedling vigor had no effect on the genetic variation underlying these fitness traits.

Molecular markers indicated a marginal decrease in genetic diversity within the S_2 population compared with the Trailhead cultivar and significant differences in pairwise φ_{ST} values between Trailhead and all random and selected populations. Additionally, nominal significant differences were detected between the S_2 and all other populations except the S_1. Our hypothesis was that neutral DNA markers would not reflect selection changes for a specific trait. That hypothesis was rejected with differences in φ_{ST} of approximately $1-2\%$ given a strict 2.5% threshold of selection (50 out of 2 500 plants). As two, or more, cycles of selection are commonly conducted for perennial grass cultivar development or improvement, this type of difference would be similar to other selection efforts in native grasses. However, these marginal changes only reflected the change in seedling vigor and establishment under a mass selection scheme, and further studies using, for example, genotypic recurrent selection would be necessary to extrapolate our results to other plant breeding methods. As an allotetraploid with disomic inheritance (Wu et al., 2003), basin wildrye is similar to self-incompatible diploid species. A possible effect of allotetraploidy on genetic variation during selection would be associated with homeologous genes under complementary gene action or linkage disequilibrium (Bingham et al., 1994), which would slow the loss of genetic variation. Although not an original goal in this study, 14 AFLP markers with significant band frequency changes in random or selected populations compared with the base population were detected. This number, corrected for multiple comparisons, is consistent with the minor changes in φ_{ST} values. While some of those 14 changed in the random populations compared with the base Trailhead cultivar, which may correspond to changes loci responding to genetic drift, 6 of those 14 markers showed changes consistent with the direction of selection and were not significant for the random versus base contrast. These six markers may be linked to genetic factors associated with seedling vigor, but further cycles of selection and QTL analyses would be necessary to confirm their tentative association.

Implications

As expected, selection for increased emergence and emergence rate from a deep seeding in basin wildrye resulted in selected populations with increased seedling vigor based on these measurements. Additionally, stringent selection for increased seedling vigor had no effect on the genetic variation underlying biomass, seed production, or stand percentage in this population. Thus, strategic selection for improvement of specific phenotypes can increase the performance of native grass species without compromising the genetics of the population.

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