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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

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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

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