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Original Research

Genecology of Thurber's Needlegrass (*Achnatherum thurberianum* [Piper] Barkworth) in the Western United States☆

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ABSTRACT

Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth) is a key restoration species in the Great Basin and surrounding areas, yet comprehensive studies of how climate relates to genetic variation and seed zones for restoration projects are lacking. Potentially adaptive phenotypic traits of 66 diverse populations of Thurber's needlegrass were measured in common gardens at Central Ferry, Washington and Reno, Nevada in 2012 and 2013. Extensive genetic variation was observed among phenology, morphology, and production traits ($P < 0.01$), and canonical correlation was used to relate traits to source climate variables. Only with the first two canonical variates were F values significant ($P < 0.05$), explaining 42% and 18% of the variation, respectively. For variates 1 and 2, strong canonical correlations of 0.97 and 0.94 linked genetic variation with source climates, providing evidence for climate-driven evolution. Pearson linear correlations indicated that populations from warmer, drier locations generally had earlier blooming and longer awns than those from cooler, wetter locations. Plants from warmer, drier locations also had higher survival at Central Ferry and higher leaf length to width (narrower leaves) at Reno in 2012. Regression of the canonical variates 1 and 2 for traits with source climate variables produced very strong models, explaining 94% and 87% of the variation in plant traits. These models were used to map 12 seed zones encompassing 465 079 km^2 in the Great Basin and surrounding areas with six seed zones representing 90% of the mapped area. We recommend using these seed zones to guide restoration of Thurber's needlegrass.

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Introduction

Evolution of adaptive genetic traits is often climate driven (Turesson 1922; Clausen et al. 1940; Aspinwall et al. 2013). When genetic variation in plant traits is correlated with source climate variables, it suggests climate-driven natural selection and evolution (Endler 1986; Kawecki and Ebert 2004; Weißhuhn et al. 2012). Natural selection often results in a "home site advantage" or local adaption associated with germplasm sources. Although there are exceptions (Galloway and Fenster 2000; Leimu and Fischer 2008; Bischoff and Mueller-Schaerer, 2010; Hancock et al. 2013), locally derived germplasm has often been shown to have an adaptive advantage compared with those from other environments. In a survey of reciprocal transplant studies, Leimu and Fischer (2008) and Hereford (2009) found the overall frequency of local adaptation measured as relative fitness was 0.71.

Given the prevalence of local adaptation in wild populations, the common practice of seeding a few selected ecotypes over large and varied geographic areas adds considerable risk of maladaptation and the potential to promote genetic swamping, genetic erosion (Hufford and Mazer 2003), outbreeding depression (Kramer and Havens 2009), and unfavorable interactions with other plant and animal species.

If conducted over the needed geographic area and timescale, direct assessments of adaptation can be accomplished through reciprocal transplant studies. With an adequate number of sites and source populations, these could be used for seed zone development; that is, the creation of geographic boundaries for appropriate germplasm movement (Wang et al. 2010). However, practical considerations usually limit the number of populations that can be included in reciprocal transplant studies (Kawecki and Ebert 2004). On the other hand, genecology studies are more easily completed using a relatively large number of source populations (St. Clair et al. 2005; Johnson et al. 2010; Johnson et al. 2012; Johnson et al. 2013; St. Clair et al. 2013; Johnson et al. 2015; Johnson and Vance-Borland 2016). Thus, the goal of genecology studies is to characterize local adaptation across a wide geographic range, and therefore sampling prioritizes collecting from as many locations as possible. To conduct a genecology study, plants from these diverse source locations are grown in common gardens to determine whether there

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is genetic variation in potentially adaptive phenotypic traits. In analyses of variation for plant traits, differences among source location phenotypes indicate genetic variation (Kawecki and Ebert 2004). Multivariate statistics are used to consolidate the traits into a small set of composite variates, and regression modeling is then used to determine if and to what extent composite variates relate to plant source climates. A strong linkage between phenotypic traits and environmental variables is evidence of adaptation, and seed transfer zones can then be mapped using geographic information system (GIS) technology. Thus, in contrast to reciprocal transplant studies, where relative fitness is compared among local and away source populations to identify local adaptation (e.g., Kawecki and Ebert 2004), genecology studies typically include many more populations from diverse environments grown in a smaller set of common gardens. By verifying and then modeling the relationship between phenotypes and environments, local adaptation is inferred and seed zones can be created and mapped.

In the absence of empirical seed zones created from either genecology studies or reciprocal transplants, provisional seed zones based only on climate may improve the probability of restoration with appropriate germplasm (Bower et al. 2014). But because genecology-based seed zones integrate genetic responses of species and populations across varied climates, they are preferred, as they provide an empirical link to local adaptation. With these empirical seed zones, land managers and native seed growers are best positioned to provide genetically appropriate germplasm for restoration projects.

The Great Basin, along with other parts of the western United States, is experiencing increasingly frequent fires, overgrazing, invasive weeds, and climate change, factors that threaten the diversity and function of ecosystems (Young and Evans 1978; Westerling et al. 2006; Erickson 2008; Davies et al. 2012). This has led to an increasing need for restoration. Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth) is a widespread perennial bunchgrass species in the Great Basin and surrounding areas (USDA, NRCS, 2006) and is an important component of many sagebrush communities dominant in much of the region. It develops relatively early in the spring and provides forage for livestock and wildlife, especially before the development of its prominent awns (USDA, NRCS, 2006). Fall burning of Thurber's needlegrass after reproductive development has minimal impact on subsequent plant production and survival (Davies and Bates, 2008), but burning during active growth can substantially reduce survival (Uresk et al. 1976). The natural wildfire cycles on the sagebrush (*Artemisia* sp.)/Thurber's needlegrass communities of the Great Basin have been shortened by the presence of downy brome (*Bromus tectorum* L.), often leading to its dominance and the need for both weed control and restoration of perennial species (Young and Evans 1978).

In this study, our aim was to develop seed zones for Thurber's needlegrass in much of the Great Basin and surrounding areas. Specific objectives were to 1) determine genetic variation of potentially adaptive traits for Thurber's needlegrass using common gardens; 2) relate genetic variation and seed source population climate though correlation, regression modeling, and GIS mapping; and 3) develop seed transfer zones to guide the choice of genetically appropriate populations of Thurber's needlegrass restoration plantings.

Methods

Population Sampling and Garden Establishment

Seeds from wild plants were collected from 66 source location populations in 2010 primarily from southwest Idaho, eastern Oregon, and northern Nevada (Figs. 1 and 2). Latitude and longitude coordinates were recorded at each source population using geographic positioning instrumentation. Elevation was estimated using the coordinates with the GTOPO30 global digital elevation model (https://lta.cr.usgs.gov/GTOPO30). For each source population, climate norms were extracted from ClimateWNA climate data rasters (Wang et al. 2012; http://www.genetics.forestry.ubc.ca/cfcg/ClimateWNA/ClimateWNA.html) for the time period spanning 1981 − 2010 using version 5.10. We used 17 climate variables designated by Wang et al. (2012) as "annual variables" including directly calculated means for annual temperature, warmest and coldest months, continentality, annual and summer precipitation, and annual and summer heat to moisture indices. Additional derived variables included frost-free days, the day of year ending the frost-free period, precipitation as snow, 30-yr minimum and maximum temperature extremes, evaporative demand indices, solar radiation, and relative humidity.

The 66 wild populations were established at two common garden sites. One site was near Central Ferry, Washington at 46.6692°N, −117.754°W (hereafter CF) and the other at the University of Nevada, Reno at 39.5394°N, −119.806°W (hereafter RE). The CF site, at 209 m above sea level (ASL), is located in the Snake River Canyon of eastern Washington state. The RE site is 1 371 m ASL and near the University of Nevada, Reno main campus. Both sites represent the dry, continental climates typical of the intermountain West and Great Basin. The 30-yr (1981 − 2010) mean annual temperature is 12.1°C at CF and 11.5°C at RE, and the 30-yr norm for precipitation is 384 mm at CF and 209 mm at RE.

In winter 2008 seeds from the 66 wild accessions were germinated in boxes (13.3 cm long, 12.7 wide, and 3.5 cm deep) containing water-saturated vermiculate. The boxes were placed at room temperature (~20°C), and seeds were allowed to germinate. Germinates were planted into 5 × 5 × 5 cm containers in flats holding 36 containers of Sunshine #5 plug mix (SunGro Horticulture, Bellevue, WA) and grown under greenhouse conditions for 6 wk. Seedlings were watered and fertilized as needed to promote optimal growth.

Seedlings were transplanted on 14 September 2011 at CF and from 5 to 10 October 2011 at RE. Six seedlings per population were planted in each of the two locations in six randomized complete blocks, resulting in a total of 792 plants included in this experiment. We note that the goal of this study is to identify broad-scale patterns of local adaptation across the range of a species, rather than to fully describe phenotypic variation within particular field locations. Thus, a relatively small number of individuals were sampled per population but across a large number of populations, which is considered the most effective way to describe patterns of local adaptation (Blanquart et al. 2013). Plants were spaced 0.6 m apart in rows separated by 1.5 m at CF; at RE all plants were spaced 0.6 m apart in all directions. With the extremely dry soil moisture conditions at RE, supplemental irrigation (≈10 mm) was required after transplanting and applied on 14 October, to ensure survival until fall rains commenced. Phenotypic data were not collected until the following spring, and thus this initial watering treatment was unlikely to affect plant phenotypes reported here. No fertilizer or additional irrigation was applied at either site.

The germplasm sources were randomized in six complete blocks at both common garden sites. In spring of 2011 and 2012, each plant was evaluated for phenology, production, and morphology traits at each site as defined in Table 1.

Statistical Analysis

Analysis of variance was completed on each plant trait (see Table 1) using the mixed procedure (Proc Mixed) in SAS/STAT version 9.2 as described in Littell et al. (1996) and Johnson et al. (2015). Replicate blocks were nested within sites (CF and RE). Thus, blocks within sites were assumed to be random. Years were treated as a repeated measure, and differences among garden sites, source populations, years, and their interactions were evaluated for each trait. Differences in phenotypes for location populations of a given trait represented genetic variation, and garden site, years, and interactions among site, year, and location represented phenotypic plasticity in trait expression (Scheiner and Goodnight 1984; Kawecki and Ebert 2004).

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