



Original Research

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

R.C. Johnson^{a,*}, E.A. Leger^b, Ken Vance-Borland^c^a US Department of Agriculture (USDA) –Agricultural Research Service (ARS), Plant Germplasm Research and Testing, Washington State University, Pullman, WA 99164, USA^b University of Nevada, Reno, Department of Natural Resources and Environmental Science, Reno, NV 89557, USA^c Conservation Planning Institute, Corvallis, OR 97330, USA

ARTICLE INFO

Article history:

Received 26 April 2016

Received in revised form 12 October 2016

Accepted 9 January 2017

Keywords:

climate

genecology

Great Basin

plant adaptation

restoration

seed zones

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 km² 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.

Published by Elsevier Inc. on behalf of The Society for Range Management.

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.

[☆] Funding was provided by the USDA-ARS; University of Nevada, Reno; and Great Basin Native Plant Project. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA.

* Correspondence: Box 646402, 59 Johnson Hall, Washington State University, Pullman, WA 99164, USA. Tel: +1 509 335 3771; fax: +1 509 335 6654.

E-mail address: rcjohnson@wsu.edu (R.C. Johnson).

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

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 through 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 1371 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 vermiculite. 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).

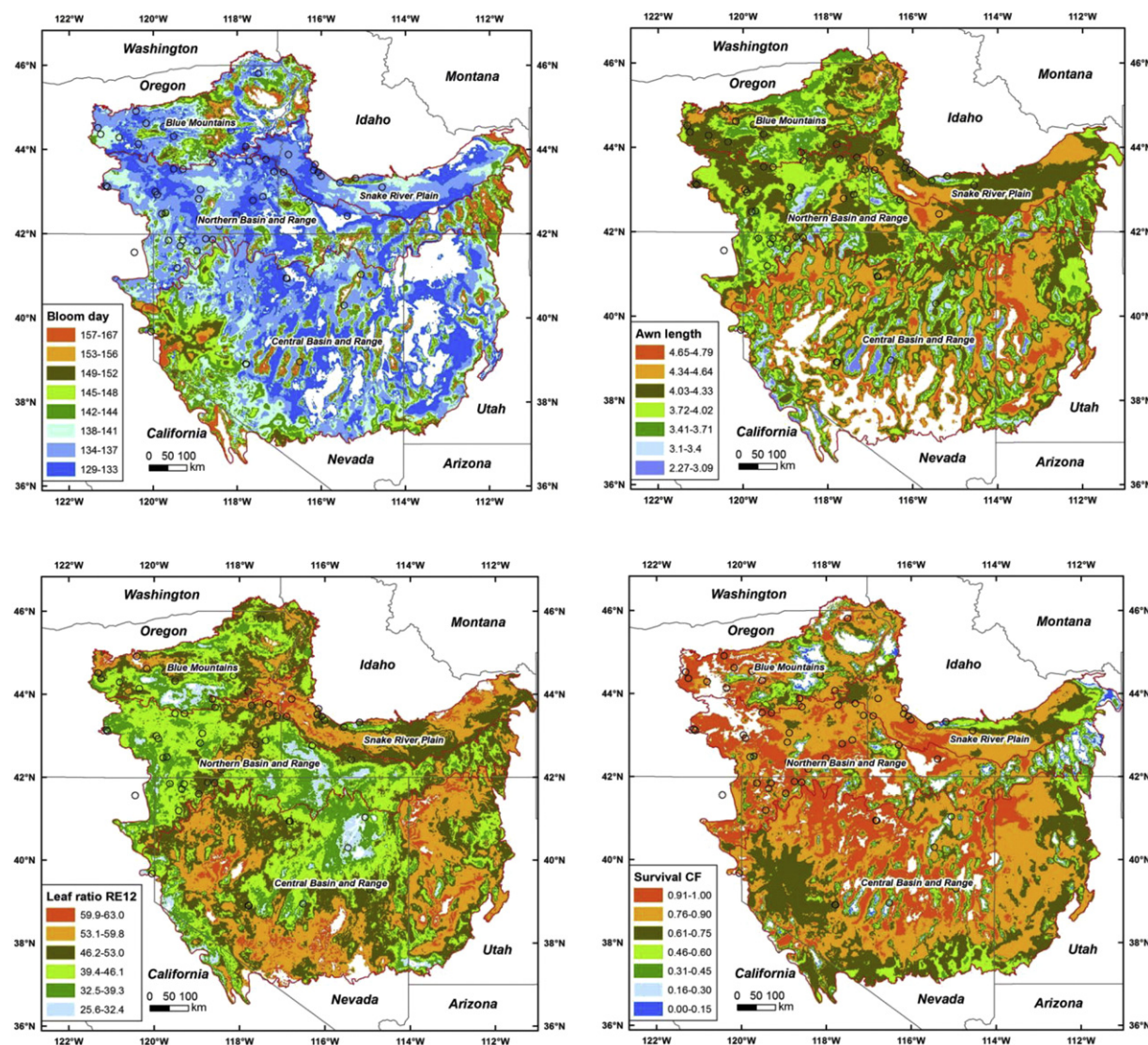


Figure 1. Maps of regression models for blooming day, awn length, leaf ratio, and survival CF with climate variables for Thurber's needlegrass in the Great Basin. Source locations for the common garden study are depicted with open circles. Omernik (1987) ecoregion boundaries are shown as black lines. Model predictions outside the trait value data range were not mapped (shown in white).

Because there were 12 plant traits measured for each population in each site and year, there was a potential of 48 traits for the canonical correlation analysis, 12 for each of the 4 site-year combinations. Such a high number of potential traits complicates the identification of a small set of canonical variates that explain a high fraction of the variation suitable for modeling with climate variables. However, averaging over interactions may discount interactions associated with phenotypic plasticity (i.e., differential responses of plant genotypes in different environments) (Bradshaw 1965). Consequently, data averaging was done only when the Pearson correlation coefficient r was highly significant and positive ($P < 0.01$) among site-year environments, indicating reasonable correspondence between traits in both magnitude and direction. Otherwise, site-year combinations were retained as separate traits.

Using this set of derived traits (Table 2), canonical correlation (PROC CANCORR in SAS/STAT version 9.2) was used to assess the relationship between traits and 17 climate variables (see Table 2) over location populations, similar to Johnson et al. (2015). This resulted in canonical variates or linear combinations of traits and climate that maximized their correlation. Each set of variates for traits and climate variables represents independent dimensions in data, with the first variate having the highest correlation and the last the lowest (Manly 1986).

Regression models for spatial mapping were developed using SAS PROC REG SAS/STAT (version 9.2). Key, single plant traits and each significant canonical variate were regressed on the climate variables (see Table 2). These models were based on a potential of 66 location populations each with 6 replications at the two garden sites evaluated for 2 yr (792 potential plants). The objective was to find models with the highest predictive value with the fewest number of model parameters (Draper and Smith 1981). Within PROC REG the R-square option was used along with the Akaike information criterion (AIC) (Akaike 1969) to minimize over parameterization. For a given trait, all climate variables from each source were initially included in the modeling process. The final model selected was the combination of climate variables that produced the highest R^2 with the lowest AIC statistic. These models maximize prediction capacity with the coefficients and variables functioning as a set, so, owing to correlations among variables in the regression, they do not necessarily identify the single most important, independent climate variables for a given trait (Manly 1986).

Spatial mapping of single traits and each significant canonical variate predicted from regression models was completed over level III Omernik ecoregions (Omernik 1987) using the grid algebra function (raster calculator) of the ArcGIS 9.3 Spatial Analyst extension (ESRI, Redlands, CA). Raster layers with the relevant climate variables were converted

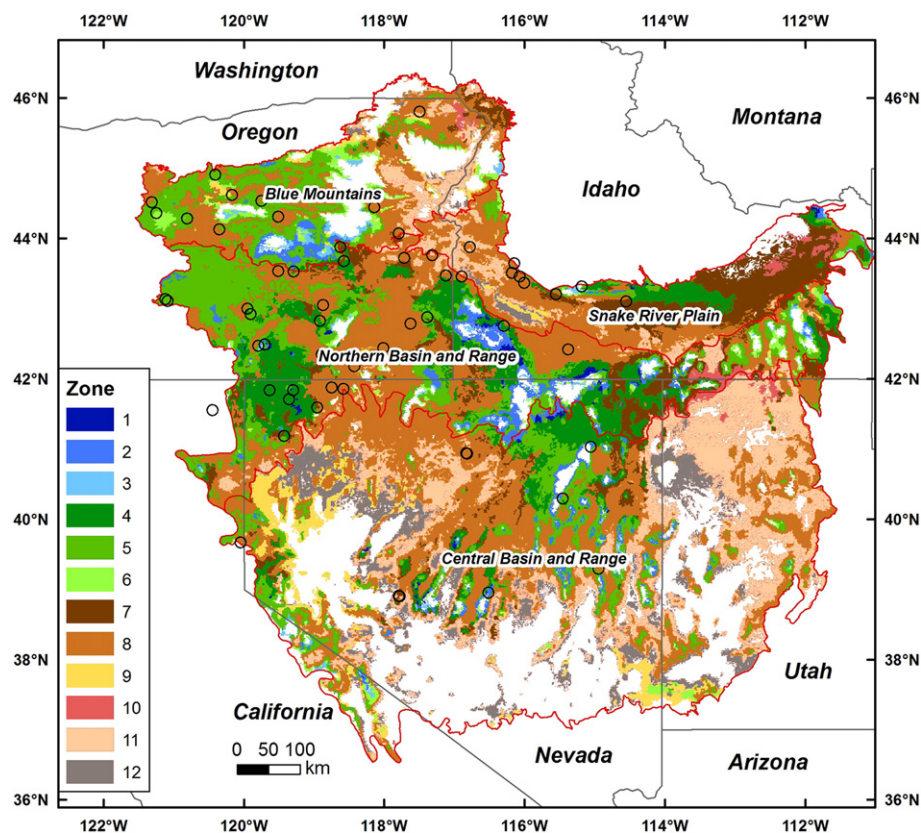


Figure. 2. Proposed seed zones for Thurber's needlegrass resulting from an overlay of canonical scores from regression models of canonical variates 1 and 2 with climate variables in the Great Basin. Source locations for the common garden study are depicted with open circles. The canonical variates were derived from canonical correlation of plant traits and climate variables. Omernik (1987) ecoregion boundaries are shown as black lines. Model predictions outside two times the data range for observed values of the canonical scores were not mapped and are shown in white.

to trait values by multiplying each climatic variable by each associated regression coefficient in the model and summing the results. The standard deviation of the regression model error term was used as the contour delimiting seed zones. Seed zone maps were developed by dividing the ranges of each set of canonical variates predicted by the regression

into segments representing different climatic areas and then overlaying those into a single seed zone map (Johnson et al. 2015). These were created over the Snake River Plain, the Northern Basin and Range, and mostly the northern sections of the Central Basin and Range, which were well represented in our seed collections.

Table 1
Summary of mean values, F-ratios (F) and P values (P) from analyses of variance for Thurber's needlegrass traits measured in common gardens sites Central Ferry, Washington and Reno, Nevada in 2012 and 2013 on diverse location populations collected from the Great Basin.

Trait	Mean	Site (S)		Loc. Pop. (L)		SxL		Yr (Y)		YxS		YxL		YxSxL	
		F	P	F	P	F	P	F	P	F	P	F	P		
Phenology ¹															
Heading, d of yr	137	27.9	<.01	8.9	<.01	2.01	<.01	187.6	<.01	27.8	<.01	0.9	0.75	1.6	0.15
Blooming, d of yr	135	17.2	<.01	6.9	<.01	1.8	<.01	78.8	<.01	2.0	0.16	1.0	0.52	0.2	0.81
Maturity, d of yr	161	36.1	<.01	3.4	<.01	1.47	0.01	2109.8	<.01	.	.	1.0	0.39	.	.
Morphology ²															
Leaf area, cm ²	1.64	263.2	<.01	4.2	<.01	1.47	0.01	125.4	<.01	147.4	<.01	0.8	0.91	0.7	0.93
Leaf ratio	74.5	41.4	<.01	1.7	<.02	1.42	0.02	27.9	<.01	85.6	<.01	1.4	0.04	1.5	<.01
Culm length, cm	37.0	715.2	<.01	3.2	<.01	2.67	<.01	98.6	<.01	0.3	0.56	0.9	0.64	1.0	0.48
Panicle length, cm	12.2	3.9	0.07	4.7	<.01	2.32	<.01	30.7	<.01	7.2	<.01	1.4	0.02	1.0	0.51
Awn length, cm	4.1	0.0	0.91	6.6	<.01	1.27	0.09	2.3	0.13	1.6	0.21	1.3	0.07	0.6	0.99
Production ³															
Survival	0.71	11.2	<.01	6.5	<.01	3.01	<.01	54.9	<.01	11.0	<.01	0.5	1.00	0.6	1.00
Panicle number	32.4	145.8	<.01	2.5	<.01	1.61	<.01	186.7	<.01	96.4	<.01	1.7	<.01	1.3	0.06
Biomass, g	12.8	230.2	<.01	3.0	<.01	2.66	<.01	17.4	<.01	14.3	<.01	1.1	0.24	1.1	0.27
Crown area, cm ²	62.8	96.5	<.01	2.0	<.01	1.67	<.01	213.0	<.01	13.7	<.01	1.1	0.30	0.9	0.79

¹ Heading was defined as complete emergence of a lead panicle from its sheath, blooming was the initial appearance of anthers, and maturity when seed appeared mature in more than half the panicles. For Reno, maturity data available only for 2012.
² Leaf area (length × width) and leaf ratio (length to width) were determined on the last fully emerged leaf of a lead culm after heading. Culm length (measured from the plant base to the base of the panicle on a lead culm), panicle length, and awn length (twice geniculate measured in three sections and summed) were measured on a lead culm after full extension.
³ Panicles on each plant were counted after heading, harvest for dry weight was after maturity to within 4 cm of the soil, and after harvest, crown area was estimated as the product of two perpendicular crown diameter measurements.

Table 2

Derived plant traits and climatic variables used in canonical correlation of Thurber's needlegrass growing at common gardens at Central Ferry (CF), Washington and Reno (RE), Nevada in 2012 and 2013.

Trait	Climatic variables
Heading	Mean average temperature (MAT)
Blooming	Mean warmest monthly temperature (MWMT)
Maturity CF	Mean coldest monthly temperature (MCMT)
Maturity RE	Continental, MWMT-MCMT (TD)
Leaf length × width (leaf area)	Mean annual precipitation (MAP)
Leaf length to width CF 2012 (leaf ratio)	Mean summer precipitation (MSP)
Leaf length to width CF 2013 (leaf ratio)	Annual heat moisture index (AHM), (MAT + 10)/(MAP/1000)
Leaf length to width RE 2012 (leaf ratio)	Summer heat moisture index (SHM), [(MWMT)/(MSP/1000)]
Leaf length to width RE 2013 (leaf ratio)	Frost-free period (FFP)
Culm length CF	D of yr when FFP ends (FFPe)
Culm length RE	Precipitation as snow (PAS)
Panicle length CF	Extreme minimum temperature over 30 yr (EMT)
Panicle length RE12	Extreme maximum temperature over 30 yr (EXT)
Panicle length RE13	Hargreaves reference evaporation (Eref)
Awn length	Hargreaves climatic moisture index (CMD)
Survival CF	Mean annual solar radiation (MAR)
Survival RE	Mean annual relative humidity (%)
Panicle number CF	
Panicle number RE	
Biomass CF	
Biomass RE	
Crown area CF	
Crown area RE 2012	
Crown area RE 2013	

Results

Differences in all traits except leaf ratio were highly significant ($P < 0.01$) among seed source populations, indicating widespread genetic variation among Thurber's needlegrass populations (see Table 1). There was also considerable phenotypic plasticity, as site and year effects were significant in almost all cases, and interactions for population × site and year × site were frequent (see Table 1).

Heading, blooming, leaf area (leaf length × width), and awn length were correlated across all site-year environments ($P < 0.01$) with positive r values (data not shown). This indicated reasonable correspondence among trait values, even when interactions between garden site and year were significant (see Table 1). Thus, those sources of phenotypic plasticity were due to changes in magnitude rather than the direction of the response of populations to garden environments. As a result, values of these traits were averaged for canonical correlation analysis (see Table 2). For other traits, values were often correlated between years within sites, and those were also averaged. Leaf ratio was the only trait for which there was no correlation for sites within year ($P < 0.01$), resulting in four separate traits. The averaging process reduced the potential of 48 to 24 derived traits (see Table 2). Those 24 derived traits were used with the 17 climate variables in Table 2 for canonical correlation analysis.

Ranges of derived traits and climates were generally large, contributing to strong differences among location populations (see Table 1). For example, the mean day of year for heading across all populations was 137, but this value ranged from 129 to 172; leaf area averaged 1.6 cm² but ranged from 0.6 to 2.7 cm² (Table S1). Geographic and climate variables were also wide ranging: elevation from 487 to 2511 m and precipitation from 701 to 213 mm (Table S2).

Canonical variates 1 and 2 (see Table S2) explained 60% of the total variation between derived traits and climate variables, 42% for variate 1 and 18% for variate 2, with P values for canonical variates 1 and 2 of $P < 0.0002$ and $P < 0.0424$, respectively. Thus canonical variates 1 and

2 established a strong link between genetic variation in common gardens and climate at source populations. No other combinations of variates were significant ($P < 0.05$) and were not considered in regression modeling.

Significant Pearson linear correlation coefficients also indicated associations between derived traits and climate, especially for blooming, awn length, leaf ratio RE 2012, and survival CF (Table 3). Although there were fewer significant relationships than for RE 2012, leaf ratio for CF 2012 (data not shown) was also correlated ($P < 0.05$) with several climate variables (MAT, MCMT, PAS, EMT, and Eref; abbreviations defined in Table 2). Thus, a link between leaf ratio and climate variables occurred at both sites in 2012. Survival RE was correlated with the climate variables AHM, PAS, EXT, Eref, and CMD (data not shown), as was survival CF (see Table 3), indicating source climate had similar effects on survival between sites.

Populations with earlier blooming were generally associated with seed source locations with higher mean and summer temperatures (MAT and MWMT), less annual precipitation (MAP), and higher stress indices (AHM and SHM) (see Table 3). Source populations from areas with generally higher temperatures (MAT, MWMT, MCMT), less annual and summer precipitation (MAP and MSP), less snow, higher evaporative demand, and higher stress indices had generally longer awns and higher survival at CF (see Table 3). Except for precipitation, source populations with narrower leaves at RE 12 showed similar trends.

Regression models with canonical variates 1 and 2 were exceptionally strong (Table 4), explaining 94% and 87% of the variation in plant phenotypes, respectively. Thus, those canonical variates effectively represented the association of plant traits and source climates, providing a strong basis for mapping seed zones. Regression models of traits for blooming, awn length, leaf ratio RE12, and survival at CF also had relatively high R^2 values (see Table 4).

Early blooming populations in common gardens (day of yr 129–137) represented a large portion of the area mapped and corresponded to the relatively warm and dry areas typical of the Great Basin (Fig. 1). Later development was predicted in relatively cooler and wetter areas such as portions of the Blue Mountains, the extreme eastern part of the Northern Basin and Range, and higher elevation areas in the Central Basin and Range. This was consistent with correlations that predicted early blooming in warmer, drier climates compared with cooler, wetter climates (see Table 3). However, a region in the west Central Basin and Range mapped to relatively late blooming (day of yr

Table 3

Pearson linear correlation coefficients between derived plant traits and canonical variates (columns) and source climate variables (rows) for Thurber's needlegrass in common gardens ($n = 60$ –64).

Climate variable ¹	Blooming	Awn length	Leaf ratio RE12	Survival CF	Can Var 1	Can Var 2
MAT	−0.38**	0.46**	0.50**	0.34**	0.49**	0.39**
MWMT	−0.32**	0.29*	0.48**	0.13	0.65**	0.03
MCMT	−0.21	0.36**	0.26*	0.40**	0.01	0.59**
TD	−0.15	0.02	0.26*	−0.14	0.58**	−0.34**
MAP	0.31*	−0.35**	−0.23	−0.49**	−0.12	−0.11
MSP	0.22	−0.26*	−0.17	−0.33**	−0.23	0.00
AHM	−0.35**	0.43**	0.37**	0.41**	0.39**	0.33**
SHM	−0.28*	0.31*	0.35**	0.27*	0.52**	0.07
FFPe	−0.16	0.12	0.45**	0.09	0.49**	0.15
FFP	−0.24	0.22	0.49**	0.10	0.57**	0.17
PAS	0.51**	−0.51**	−0.40**	−0.67**	−0.27*	−0.48**
EMT	−0.20	0.31*	0.34**	0.32**	0.06	0.54**
EXT	−0.49**	0.53**	0.37**	0.33**	0.41**	0.19
Eref	−0.34**	0.49**	0.35**	0.34**	0.39**	0.34**
CMD	−0.39**	0.48**	0.34**	0.42**	0.44**	0.21
MAR	0.32**	−0.28*	0.02	−0.26*	0.17	−0.18
RH	0.17	−0.26*	0.08	−0.21	0.15	0.02

*, ** Significance at $P < 0.05$ and $P < 0.01$, respectively.

¹ Annual climatic variables as given by Wang et al. (2012); see Table 2 for definitions of abbreviations.

Table 4
Equations and coefficients of determination (R^2) for regression of derived plant traits (represented as canonical variates or as individual traits) with climate variables at source population locations for Thurber's needlegrass.

Trait	R^2	Regression equations ¹
Canonical variate 1	0.94	$-71.295 + 2.1204 (\text{MAT}) + 1.49276 (\text{MWMT}) - 2.70608 (\text{MCMT}) - 2.78967 (\text{TD}) + 0.01837 (\text{MAP}) + 0.10983 (\text{MSP}) - 0.06846 (\text{AHM}) - 0.03372 (\text{PAS}) - 0.69977 (\text{EMT}) - 0.0665 (\text{Eref}) + 0.10238 (\text{CMD}) + 0.70136 (\text{RH})$
Canonical variate 2	0.87	$-76.529 + 6.37187 (\text{MAT}) - 2.12495 (\text{MWMT}) - 0.00648 (\text{MAP}) + 0.10021 (\text{AHM}) - 0.01778 (\text{SHM}) + 0.08954 (\text{eFFP}) - 0.12493 (\text{FFP}) + 0.07677 (\text{PAS}) - 0.92346 (\text{EMT}) + 0.49644 (\text{RH})$
Blooming	0.61	$350.33 - 0.09408 (\text{MAP}) + 0.10087 (\text{SHM}) - 0.63142 (\text{eFFP}) + 0.24391 (\text{FFP}) + 0.17409 (\text{PAS}) - 3.38374 (\text{EXT}) + 0.24648 (\text{Eref}) - 0.24346 (\text{CMD})$
Awn length	0.48	$-10.811 - 0.28074 (\text{MWMT}) + 0.01397 (\text{MSP}) + 0.02996 (\text{eFFP}) + 0.25081 (\text{EXT}) - 0.00578 (\text{Eref}) + 0.00916 (\text{CMD})$
Leaf ratio RE12	0.53	$332.92 - 12.8109 (\text{MCMT}) + 0.26948 (\text{MSP}) + 1.32273 (\text{eFFP}) + 7.94851 (\text{EMT}) - 3.83538 (\text{EXT}) - 0.18579 (\text{Eref}) + 0.18277 (\text{CMD}) - 4.81628 (\text{RH})$
Survival CF	0.66	$-6.61382 + 0.00312 (\text{MAP}) + 0.02691 (\text{eFFP}) - 0.01766 (\text{FFP}) - 0.00866 (\text{PAS}) + 0.09104 (\text{EXT}) - 0.00478 (\text{Eref}) + 0.0039 (\text{CMD})$

¹ Regression models were significant at $P < 0.0001$. Annual climatic variables as given by Wang et al. (2012) and at <http://www.genetics.forestry.ubc.ca/cfcg/ClimateWNA/ClimateWNA.html>; see Table 2 for definitions of abbreviations.

145–157 shown as red orange, yellow, and light green hues) even though it is an area considerably warmer and drier than much of the central and northern areas of the Central Basin and Range.

Longer awns, greater leaf ratios, and higher survival in common gardens generally mapped to populations from warmer, drier areas (see Fig. 1). For awn length there was a sharp transition from longer awns in the Central Basin and Range to shorter awns along much of its border with the Northern Basin and Range. High leaf ratios, or relatively narrow leaves, predominated in the warm, dry areas of the Snake River Plain and Central Basin and Range with relatively high heat moisture indices. Relatively wide leaves with smaller leaf ratios were associated with mostly cooler, wetter areas of Blue Mountain, Northern Basin and Range, and Central Basin and Range ecoregions (see Fig. 1). For most of the mapped area, survival was usually higher for populations from relatively warmer, drier regions, such as eastern Oregon in the Northern Basin and Range, and the Snake River Plain. This was also true in most of the Central Basin and Range (see Fig. 1).

The seed zone map was developed by dividing the range of canonical scores predicted by regression models into segments and then overlaying the segments representing the different canonical variates. Regression with canonical scores for variate 1 was divided into 4 segments and those for variate 2 into 3 segments, resulting in an overlay with 12 seed zones (Fig. 2). Canonical variate 1 was given somewhat more weight than variate 2 as it explained more of the total trait variation. The seed zone map was focused in the Snake River Plain, the Northern Basin and Range, and mostly northern sections of the Central Basin and Range. Much of the western, eastern, and southern Central Basin and Range and significant portions of the Blue Mountains were outside our designated mapping range of two times the observed canonical scores used to prevent excessive model extrapolation. A total of 465 079 km² was mapped. Of the 12 zones, 6 (zones 1, 2, 3, 6, 9, and 10) represented less than 10% of the total mapped area (see Fig. 2). The remaining six zones represented 90% of the mapped areas with three zones, 5 (15.2%), 7 (17.7%), and 8 (33.4%) representing 66.3%.

Plots of zone mean temperature and precipitation illustrated how our trait-based approach created zones separated by different climates (Fig. 3). The low stress zone 3 (with relatively lower temperature and higher precipitation) represented a small portion of the total area (0.8%). It was scattered mostly in parts of the Blue Mountain ecoregion but to some extent in other ecoregions, corresponding to generally higher elevation areas (see Fig. 2). The high stress zone 12 (higher temperature and lower precipitation), most frequently in the highly arid and hot areas in the Central Basin and Range, represented 7.2% of the mapped area. It was often bordered by zones 11 (7.25% of the mapped area) and 9 (3.2% of the area), two other relatively high stress zones (see Fig. 3). Zone 8, representing a third of the mapped area, was distributed in all ecoregions of the Great Basin. Zones 4, 7, and 10 were closely grouped in terms of precipitation and temperature and often mapped to adjacent areas (see Fig. 2).

Discussion

We found strong evidence that natural selection has affected plant phenotypes of Thurber's needlegrass in the intermountain West. Nearly all potentially adaptive plant traits differed significantly among location populations in common gardens, indicating considerable genetic variation within this species. This is consistent with research on other grasses and forbs from the Great Basin and intermountain West (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) and is generally observed in common garden research in other species and regions (St. Clair et al. 2005; Leimu and Fischer 2008; Horning et al. 2010).

Significant Pearson linear correlations between derived traits and climate variables suggested an association between traits and certain climate variables, even though they did not represent a large part of the total variation. In contrast, the canonical correlation analysis between derived traits and climates resulted in the first two canonical variates explaining 60% of the variation, strongly linking genetic variation with source climatic factors and suggesting climate-driven natural selection and evolution leading to local adaptation. This was comparable or somewhat stronger than for other genecology studies of bunchgrasses using multivariate traits (Erickson et al. 2004; Johnson et al. 2010; Johnson et al. 2012; St Clair et al. 2013; Johnson et al. 2015; Johnson and Vance-Borland 2016).

Interactions between source populations and different site and year garden environments showed the expected presence of phenotypic plasticity observed in similar studies on other species (Johnson et al.

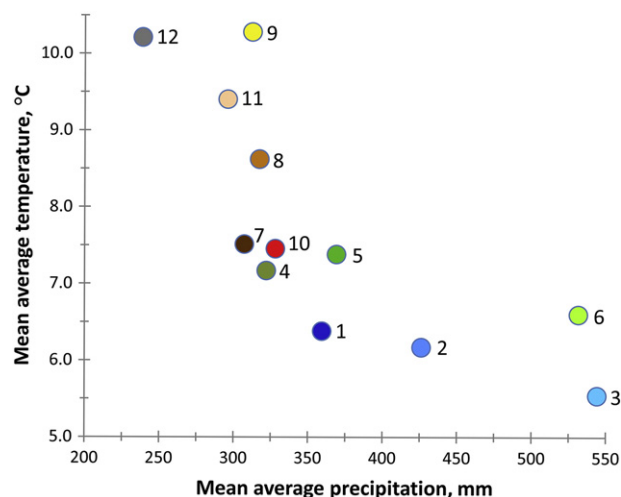


Figure 3. Relationship between average temperature and precipitation for Thurber's needlegrass seed zones in the intermountain West.

2013; St Clair et al. 2013; Johnson et al. 2015; Johnson and Vance-Borland 2016). In basin wildrye (*Leymus cinereus* [Scribn. & Merr.] A. Love), plasticity usually represented a large fraction of the variation but also varied for a given trait (Johnson and Vance-Borland, 2016); there are likely corollaries with Thurber's needlegrass. Still, there were frequent, positive linear correlations among sites and years, indicating that interactions were due mostly to changes in magnitude of responses, rather than in direction.

Mechanisms that promote adaption to stressful environments can be described as escape (growth and development when stress is less severe), avoidance (the external stress is present but the plant avoids equilibrium with it), and tolerance (the external stress approaches equilibrium with the stress but plant metabolic function is maintained at some level) (Levitt 1972). The trend toward early phenology in climates with lower precipitation and high evapotranspiration potential is consistent with drought stress escape mechanisms (Levitt 1972). Specifically, earlier blooming populations were found in areas with warmer, drier source climates (see Table 3), and that was also seen in most of the regions when mapped (see Fig. 1). Earliness as a form of escape was also observed with bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Å. Löve) (St. Clair et al. 2013), Sandberg bluegrass (*Poa secunda*) (Johnson et al. 2015), and basin wildrye (Johnson and Vance-Borland 2016) from high-stress areas in the intermountain West. Selection for early flowering individuals was also observed in a field study with the native perennial grass bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey) (Kulpa and Leger 2013). However, contrary to these results, late blooming mapped to a very hot and dry area in the west-central Basin and Range. Given that populations were not actually collected in that specific area, this result should be interrupted with caution. Since that area was outside the mapped range for the seed zones, there was no impact on seed movement guidelines (see Fig. 2).

The generally longer awns in location populations from warmer, drier areas are also consistent with their reported role in stress avoidance. In cereal crops, awns have been shown to promote photosynthesis, transpirational cooling, and sensible heat loss during seed development under drought and high temperature stress (Evans et al. 1972; Ferguson et al. 1973; Blum 1986; Motzo and Giunta 2002). As shown in wild wheat (*Triticum turgidum* ssp. *diccoides*), awns also have a potential function in seed dispersal and in promoting seedling recruitment by helping propel seeds into the ground (Elbaum et al. 2007). The correlation of relatively narrow leaves (leaf ratios) with populations from higher temperature sources suggests heat dissipation and water conservation attributes also consistent with stress avoidance. A similar result for leaf ratio was found in bluebunch wheatgrass (St Clair et al. 2013) and Sandberg bluegrass (Johnson et al. 2015) in the intermountain West including the Great Basin. Thus, both stress escape and avoidance appear to be key mechanisms in the adaptation of Thurber's needlegrass and other bunchgrasses of the intermountain West to higher-stress environments. Still, the presence of escape and avoidance mechanisms does not exclude stress tolerance mechanisms. Stress tolerance in populations from warm, dry regions was beyond the scope of this study but represents a research opportunity.

The regression models for canonical variates 1 and 2 with climate variables were substantially higher than other studies of perennial bunchgrasses in the intermountain West. (Erickson et al. 2004; Johnson et al. 2010; Johnson et al. 2012; St Clair et al. 2013; Johnson et al. 2015) (Table 4). Horning et al. (2010), working with oceanspray (*Holodiscus discolor* [Pursh] Maxim.), reported a regression model based on plant traits from the first principal component with a R^2 of 0.86, which is the only study found that approached the strength of our models for Thurber's needlegrass. Thus, the strong regression models for Thurber's needlegrass indicated that canonical variates 1 and 2, as composite plant traits, were closely associated with climate differences across much of the Great Basin and surrounding areas.

Self-pollination is common in closely related species including Indian ricegrass (*Achnatherum hymenoides* [Roem. & Schult]

Barkworkth = *Stipa hymenoides*) (Jones and Nielson 1989). But as far as we know, the potential for outcrossing in Thurber's needlegrass has not been fully assessed. Differences in mating system, gene flow, population size, phenotypic plasticity, and genetic diversity all affect the potential for population differentiation (Hamrick and Godt, 1996; Charlesworth and Wright 2001; Garant et al. 2007; Scheiner and Holt 2012), and further studies relating these factors to the degree of local adaptation observed in co-occurring Great Basin species would be highly instructive.

It is important to note that seed zone borders are to an extent arbitrary and can be modified on the basis of new information and knowledge of land managers. In some cases smaller-scale restoration may be desired for specific needs and local microclimates may require a more site-specific approach. More mapping detail could be achieved by dividing the range of canonical variates into more sections. This could allow more precise guidance to smaller areas, but across the Great Basin, it would rapidly increase the number of zones and cost of additional collection and seed increase. In the current seed zone map, as in similar studies (Johnson et al. 2015; Johnson and Vance-Borland 2016), we sought to balance seed zone size with the practical needs for application on relatively large-scale restoration projects. Further field testing could identify areas where seed zones could be collapsed or divided, as needed.

Applying this balanced approach for Thurber's needlegrass resulted in six zones (4, 5, 7, 8, 11, and 12) that represented 90% of the mapped area and predominated in semiarid to arid climates. The wetter and cooler zones (1, 2, 3, and 6) represented just 6% of the mapped area and are less likely to require active restoration, as more mesic areas of the Great Basin are typically more resilient to disturbance (Chambers et al., 2013). For zones 4, 7, and 10, the relatively small differences in climate had enough effect on genetic traits to result in different seed zones (see Fig. 3). Still, those zones were often juxtaposed, suggesting potential coalescence could be considered by land managers. Moreover, reciprocal transplants across these zones could determine the magnitude of decline in performance, if any, associated with seed movement among seed zones. Overall, the number of populations needed for restoration by zones is within practical limits. This has also been the case in other genecology studies on perennial bunchgrasses in the intermountain West (Johnson et al. 2010; Johnson et al. 2012; St. Clair et al. 2013; Johnson et al. 2015). Likely more limiting to seed availability of Thurber's needlegrass are difficulties in seed cleaning presented by the extensive awns, which are longer in populations from the warmer, drier seed zones most in need of restoration. Although initially more labor intensive, transplanting seedlings is a way to obtain more viable, surviving plants with fewer seeds and may be a way to minimize problems associated with seed awns.

Since the scope for future selective adaption and evolution depends on the availability of genetic variation (Sgrò et al. 2011), we also recommend numerous wild populations be collected and used as a restoration population within seed zones. This may be especially important when large distances and ecoregions separate seed zones. For example, zone 11 occurs in the western Snake River Plain and also in the western and eastern Central Basin and Range. A conservative approach would be to restrict seed movement between such distant areas as a buffer against factors not directly considered, such as biotic stresses, establishment potential, and soils. That approach would also require bearing the cost of more restoration populations. Such decisions require consideration by land managers consistent with available resources and experience.

Finally, due to practical issues associated with establishing plants from seed, we note that these seed zones were developed on the basis of plant responses measured from the seedling stage to maturity. In our study, genetic variation was observed during the establishment phase as higher survival and was associated with higher stress location populations, but germination and emergence were not directly considered. Thurber's needlegrass does not possess the dormancy typical of

Indian ricegrass but has been observed to have relatively low germination rates and seedling vigor (Martens et al. 1994; USDA and NRCS, 2006). Attempting to complete a genecology study of adaptive traits in growth and development from seeds would in all probability result in many location populations that do not germinate, emerge, or establish confounding efforts to study later growth stages, and thus, those stages were not fully considered here.

Further testing of seed zones in field situations could be conducted using seedling emergence and survival as response variables, and additional studies could be conducted to ask how well seed and seedling traits correlate with adult phenotypes. For example, using seed collected from different field environments, Espeland and Hammond (2013) found that Sandberg bluegrass seed emergence and early dry weight in growth chambers were positively correlated with dry weight after 19–20 wk of additional growth in a greenhouse environment. Therefore, we encourage studies of plant germination, emergence, and establishment within the context of the seed zones, asking whether seedling establishment can be predicted on the basis of phenotypes at later growth stages. Given that genetic variation in growth and development of plant traits was strongly linked to climate, perhaps differences in seedling recruitment would also be linked.

Implications

Land managers are challenged to identify populations for large-scale restoration projects that are adapted and ecologically suited over diverse regions. In this study 12 seed zones were developed to guide restoration for Thurber's needlegrass according to the relationship between genetic variation in common gardens and seed source climates. There was a strong link between climate and key plant traits, suggesting climate-driven evolution and adaptation. Because only six seed zones represented 90% of the mapped area, seed production of populations by zone would be practical even though large-scale seed processing would be complicated by the typically long awns of this species. Seed zones should be open to revision and modification consistent with future research, climate change, and local knowledge of Thurber's needle grass adaptation. Still, they provide a research-based framework for selecting Thurber's needlegrass seed sources for restoration projects over much of the intermountain western United States.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.rama.2017.01.004>.

Acknowledgments

We are grateful to Melissa Scholten, Mike Cashman, and Walter Kaiser for their work in seed and data collection in Central Ferry, Washington, along with Bryce Wehan, Lyndsey Boyer, Meghan Whitman, Brittany Trimble, and Riley Anderson for their assistance in the Reno, Nevada common garden.

References

- Akaike, H., 1969. Fitting autoregressive models for prediction. *Annals of the Institute of Statistical Mathematics* 21, 243–247.
- Aspinwall, M.J., Lowry, D.B., Taylor, S.H., Juenger, T.E., Hawkes, C.V., Johnson, M.-V.V., Kiniry, J.R., Fay, P.A., 2013. Genotypic variation in traits linked to climate and above-ground productivity in a widespread C-4 grass: evidence for a functional trait syndrome. *New Phytologist* 199, 966–980.
- Bischoff, A., Mueller-Schaerer, H., 2010. Testing population differentiation in plant species—how important are environmental maternal effects? *Oikos* 119, 445–454.
- Blanquart, F., Koltz, O., Nuismer, S.L., Gandon, S., 2013. A practical guide to measuring local adaptation. *Ecology Letters* 16, 1195–1205.
- Blum, A., 1986. The effect of heat-stress on wheat leaf and ear photosynthesis. *Journal of Experimental Botany* 37, 111–118.
- Bower, A.D., Clair, B.St., Erickson, V., 2014. Generalized provisional seed zones for native plants. *Ecology Applications* 24, 913–919.
- Bradshaw, A.D., 1965. Evolutionary significance of phenotypic plasticity in plants. *Advanced Genetics* 13, 115–1555.
- Chambers, J.C., Bradley, B.A., Brown, C.S., D'Antonio, C., Germino, M.J., Grace, J.B., Hardegree, S.P., Miller, R.F., Pyke, D.A., 2013. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of Western North America. *Ecosystems* 17, 360–375.
- Charlesworth, D., Wright, S.I., 2001. Breeding systems and genome evolution. *Current Opinions in Genetic Development* 11, 685–690.
- Clausen, J., Keck, D.D., Hiesey, W.M., 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Institute, Washington, DC, USA (Publication 520).
- Davies, G.M., Bakker, J.D., Dettweiler-Robinson, E., Dunwiddie, P.W., Hall, S.A., Downs, J., Evans, J., 2012. Trajectories of change in sagebrush steppe vegetation communities in relation to multiple wildfires. *Ecological Applications* 22, 1562–1577.
- Davies, K.W., Bates, J.D., 2008. The response of Thurber's needlegrass to fall prescribed burning. *Rangeland Ecology & Management* 61, 188–193.
- Draper, N.R., Smith, H., 1981. *Applied regression analysis*. second ed. Wiley, New York, NY, USA.
- Elbaum, R., Zaltzman, L., Burgert, I., Fatzl, P., 2007. The role of wheat awns in the seed dispersal unit. *Science* 316, 884–886.
- Endler, J.A., 1986. Natural selection in the wild. *Monographs in Population Biology* 21, 1–336.
- Erickson, V.J., 2008. Developing native plant germplasm for national forests and grasslands in the Pacific Northwest. *Native Plants Journal* 9, 255–266.
- Erickson, V.J., Mandel, N.L., Sorensen, F.C., 2004. Landscape patterns of phenotypic variation and population structuring in a selfing grass, *Elymus glaucus* (blue wildrye). *Canadian Journal of Botany* 82, 1776–1789.
- Espeland, E.K., Hammond, D., 2013. Maternal effects on growth and competitive ability in a commonly used restoration species. *Native Plants Journal* 14, 213–242.
- Evans, L.T., Bingham, J., Jackson, P., Sutherland, J., 1972. Effect of awns and drought on the supply of photosynthate and its distribution within wheat ears. *Annals of Applied Biology* 70, 67–76.
- Ferguson, H., Eslick, R.F., Aase, J.K., 1973. Canopy temperatures of barley as influenced by morphological characteristics. *Agronomy Journal* 65, 425–428.
- Galloway, L.F., Fenster, C.B., 2000. Population differentiation in an annual legume: local adaptation. *Evolution* 54, 1173–1181.
- Garant, D., Forde, S.E., Hendry, A.P., 2007. The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology* 21, 434–443.
- Hamrick, J.L., Godt, M.J.W., 1996. Effects of life history traits on genetic diversity in plant species. *Philosophical Transactions of the Royal Society of London Series B Biological Sciences* 351, 1291–1298.
- Hancock, N., Leishman, M.R., Hughes, L., 2013. Testing the "local provenance" paradigm: a common garden experiment in Cumberland Plain Woodland, Sydney, Australia. *Restoration Ecology* 21, 569–577.
- Hereford, J., 2009. A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist* 173, 579–588.
- Horning, M.E., McGovern, T.R., Darris, D.C., Mandel, N.L., Johnson, R., 2010. Genecology of *Holodiscus discolor* (Rosaceae) in the Pacific Northwest, USA. *Restoration Ecology* 18, 235–243.
- Hufford, K.M., Mazer, S.J., 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecological Evolution* 18, 147–155.
- Johnson, R.C., Cashman, M.J., Vance-Borland, K., 2012. Genecology and seed zones for Indian ricegrass collected in the southwestern United States. *Rangeland Ecology Management* 65, 523–532.
- Johnson, R.C., Erickson, V.J., Mandel, N.L., Clair, J.B.St., Vance-Borland, K.W., 2010. Mapping genetic variation and seed zones for *Bromus carinatus* in the Blue Mountains of eastern Oregon, USA. *Botany-Botanique* 88, 725–736.
- Johnson, R.C., Hellier, B.C., Vance-Borland, K.W., 2013. Genecology and seed zones for tapertip onion in the US Great Basin. *Botany-Botanique* 91, 686–694.
- Johnson, R.C., Horning, M.E., Espeland, E.K., Vance-Borland, K., 2015. Relating adaptive genetic traits to climate for Sandberg bluegrass from the intermountain western United States. *Evolution Applications* 8, 172–184.
- Johnson, R.C., Vance-Borland, K., 2016. Linking genetic variation in adaptive plant traits to climate in tetraploid and octoploid basin wildrye (*Leymus cinereus* [Scribn. & Merr.] A. Love) in the western U.S. *PLoS One* 11. <http://dx.doi.org/10.1371/journal.pone.0148982>.
- Jones, T.A., Nielson, D.C., 1989. Self-compatibility in Paloma Indian ricegrass. *Journal of Range Management* 42, 187–190.
- Kawecki, T.J., Ebert, D., 2004. Conceptual issues in local adaptation. *Ecology Letters* 7, 1225–1241.
- Kramer, A.T., Havens, K., 2009. Plant conservation genetics in a changing world. *Trends Plant Science* 14, 599–607.
- Kulpa, S.M., Leger, E.A., 2013. Strong natural selection during plant restoration favors an unexpected suite of plant traits. *Evolution Applications* 6, 510–523.
- Leimu, R., Fischer, M., 2008. A meta-analysis of local adaptation in plants. *PLoS One* 3. <http://dx.doi.org/10.1371/journal.pone.0004010>.
- Levitt, J., 1972. Responses of plants to environmental stresses. Academic Press, New York, NY, USA (697 pp.).
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., 1996. SAS system for mixed models. SAS Institute, Inc., Cary, NC, USA.
- Manly, B.F.J., 1986. Multivariate statistical methods: a primer. Chapman Hall, New York, NY, USA (224 pp.).
- Martens, E., Palmquist, D., Young, J.A., 1994. Temperature profiles for germination of cheatgrass versus native perennial bunchgrasses. In: Monsen, S.B., Kitchen, S.G. (Eds.), *Proceedings—ecology and management of annual rangelands*; 1992 May 18–22; Boise, ID. Gen. Tech. Rep. INT-GTR-313. US Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT, pp. 238–243.
- Motzo, R., Giunta, F., 2002. Awnedness affects grain yield and kernel weight in near-isogenic lines of durum wheat. *Australian Journal of Agricultural Research* 53, 1285–1293.

- Omerik, J.M., 1987. Ecoregions of the conterminous United States. *Annals of Association of American Geography* 77, 118–125.
- Scheiner, S.M., Goodnight, C.J., 1984. The comparison of phenotypic plasticity and genetic variation in populations of the grass *Danthonia spicata*. *Evolution* 38, 845–855.
- Scheiner, S.M., Holt, R.D., 2012. The genetics of phenotypic plasticity. X. Variation versus uncertainty. *Ecology and Evolution* 2, 751–767.
- Sgrò, C.M., Lowe, A.J., Hoffmann, A.A., 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evolution Applications* 4, 326–337.
- St. Clair, J.B., Kilkenny, F.F., Johnson, R.C., Shaw, N.L., Weaver, G., 2013. Genetic variation in adaptive traits and seed transfer zones for *Pseudoroegneria spicata* (bluebunch wheatgrass) in the northwestern United States. *Evolution Applications* 6, 933–948.
- St. Clair, J.B., Mandel, N.L., Vance-Boland, K.W., 2005. Genecology of Douglas fir in western Oregon and Washington. *Annals of Botany* 96, 1199–1214.
- Turesson, G., 1922. The genotypical response of the plant species to the habitat. *Hereditas* 3, 211–350.
- Uresk, D.W., Cline, J.F., Rickard, W.H., 1976. Impact of wildfire on three perennial grasses in south-central Washington. *Journal of Range Management* 29, 309–310.
- USDA, NRCS, 2006. The PLANTS Database, Version 061010. (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA, USA.
- Wang, T., Hamann, A., Spittlehouse, D.L., Murdock, T.Q., 2012. ClimateWNA-High-Resolution Spatial Climate Data for Western North America. *Journal of Applied Meteorology Climatology* 51, 16–29.
- Wang, T., O'Neill, G.A., Aitken, S.N., 2010. Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecology Applications* 20, 153–163.
- Weißhuhn, K., Prati, D., Fischer, M., Auge, H., 2012. Regional adaptation improves the performance of grassland plant communities. *Basic Applied Ecology* 13, 551–559.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. *Science* 313, 940–943.
- Young, J.A., Evans, R.A., 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* 31, 283–289.