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Mapping genetic variation and seed zones for *Bromus carinatus* in the Blue Mountains of eastern Oregon, USA[1]

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Abstract: Seed transfer zones ensure that germplasm selected for restoration is suitable and sustainable in diverse environments. In this study, seed zones were developed for mountain brome (*Bromus carinatus* Hook. & Arn.) in the Blue Mountains of northeastern Oregon and adjoining Washington. Plants from 148 Blue Mountain seed source locations were evaluated in common-garden studies at two contrasting test sites. Data on phenology, morphology, and production were collected over two growing seasons. Plant traits varied significantly and were frequently correlated with annual precipitation and annual maximum temperature at seed source locations ($P < 0.05$). Plants from warmer locations generally had higher dry matter production, longer leaves, wider crowns, denser foliage, and greater plant height than those from cooler locations. Regression models of environmental variables with the first two principal components (PC 1 and PC 2) explained 46% and 40% of the total variation, respectively. Maps of PC 1 and PC 2 generally corresponded to elevation, temperature, and precipitation gradients. The regression models developed from PC 1 and PC 2 and environmental variables were used to map seed transfer zones. These maps will be useful in selecting mountain brome seed sources for habitat restoration in the Blue Mountains.

Key words: genecology, *Bromus carinatus*, seed zones, plant adaptation.

Résumé : Les zones de transfert des semences assurent qu'un germoplasme sélectionné pour la restauration convient et demeure durable dans divers environnements. Dans cette étude, les auteurs ont développé des zones d'ensemencement pour le brome (*Bromus carinatus* Hook. & Arn.) des Blue Mountains du nord-est de l'Oregon et de l'état de Washington voisin. Dans des jardins communs situés sur deux sites fortement contrastés, ils ont évalué des plants provenant de 148 provenances de semences récoltées dans les Blue Mountains. Ils ont réuni les données sur la phénologie, la morphologie et la productivité au cours de deux saisons de croissance. Les caractères des plantes varient significativement et montrent souvent des corrélations avec la précipitation annuelle et les températures maximales annuelles prévalant sur les sites de provenance des semences. Les plantes venant des localités plus chaudes montrent généralement une productivité en matière sèche plus grande, des feuilles plus longues, des cimes plus larges, un feuillage plus dense et des plants plus hauts, que ceux provenant de localités plus froides. Les modèles de régression des variables environnementales portant sur les deux premières composantes principales (PC 1 et PC 2) expliquent respectivement 46 % et 40 % de la variation totale. Les cartes des PC 1 et PC 2 correspondent généralement aux gradients d'élévation, de température et de précipitation. Les auteurs ont utilisé les modèles de régression développés à partir des PC 1 et PC 2 avec les variables environnementales pour cartographier les zones de transfert des sources de semences destinées à la restauration des habitats dans les Blue Mountains.

Mots-clés : génécologie, *Bromus carinatus*, zones des semences, adaptation végétale.

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Introduction

Native forest and rangeland plant communities are increasingly threatened by overgrazing (Belsky and Blumenthal 1997), uncharacteristic frequent wildfires (Hessburg et al. 2005), invasive weeds (Mack 1981; Keeley 2006), and climate change (Westerling et al. 2006). As the need for restoration increases, the choice of plant materials becomes in-

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creasingly critical. A number of studies have shown that in most cases, locally derived germplasm is best adapted to the prevailing climate and environmental conditions (Knapp and Rice 1996; Hufford and Mazer 2003; Rice and Knapp 2008). The use of "local" germplasm, however, is hampered by lack of a lack of knowledge concerning "how local is local?" (McKay et al. 2005). If the germplasm used for restoration originates from an overly restricted area, resources for restoration are wasted and the process is unduly cumbersome. On the other hand, if the germplasm is not "local" enough, it may perform poorly in restoration plantings and potentially erode the genetic diversity of remnant populations through hybridization and introgression (Hufford and Mazer 2003; McKay et al. 2005).

Reciprocal transplant studies are effective in demonstrating local adaptation (Rice and Knapp 2008). They have the advantage of testing plants in their "home" environment against "away" environments (Kawecki and Ebert 2004). However, they are limited by the relatively small number of experimental test sites and seed sources that can normally be evaluated over a region of interest. Alternatively, germplasm collected from a relatively large number of locations over a region and evaluated in common-garden studies has been effectively used to develop seed transfer zones (delineated areas within which movement of plants will not compromise adaptation) (Campbell 1986; Sorensen 1992; Rehfeldt 1994). The disadvantage is that a direct test of local adaptation is not possible. Nevertheless, when strong and interpretable correlations are detected between genetic variation and environmental variables across seed source locations, the variation observed in common-garden experiments is usually assumed to result from natural selection and adaptation rather than random forces such as drift (Heslop-Harrison 1964; Endler 1986).

Past seed zone research has principally focused on commercially important tree species; much less is known concerning genetic diversity and the appropriate scale of plant movement in native shrub, grass, and forb species (Hufford and Mazer 2003; Johnson et al. 2004; McKay et al. 2005). For native perennial grasses, local adaptation has been demonstrated in *Elymus glaucus* (blue wildrye) and *Nassella pulchra* (purple needlegrass) (Knapp and Rice 1996; Rice and Knapp 2008). Erickson et al. (2004) developed seed zones based on the geographic subdivisions of blue wildrye in the Blue Mountains of southeastern Washington and northeastern Oregon. Kitzmiller (2009) found that plant traits varied widely in a common-garden study with blue wildrye, Orcutt's brome (*Bromus orcuttianus* Vasey), and mountain brome [also known as California brome (*Bromus carinatus* Hook. & Arn. = *Bromus marginatus* Nees ex Steud.)]. However, we know of no studies in which seed zones have been developed for mountain brome.

Mountain brome is a native, predominantly cleistogamous, octaploid ($2n = 56$) cool season perennial bunchgrass with a wide distribution throughout western North America (Harlan 1945*a*, 1945*b*; Hitchcock et al. 1969; Hickman 1993). It is generally adapted to deep soils of medium to fine texture but occurs at a wide range of elevation, temperature, and precipitation zones. The species has a number of attributes that make it well-suited for the restoration of disturbed sites, including rapid establishment and deep, widespreading roots that promote soil stabilization (Hassell et al. 1983). As a result, mountain brome is increasingly being collected and propagated for use in restoration in a number of regions, including the Blue Mountains of northeastern Oregon and southeastern Washington.

Several mountain brome cultivars have been developed from North American sources, including 'Bromar' (1946), 'Cucamonga' (1949), and 'Garnet' (2001) (USDA 2006). 'Bromar' is the most prominent and extensively used mountain brome cultivar in the Pacific Northwest. Although its specific geographic origin is uncertain, 'Bromar' was chosen from among 154 accessions collected in the western US and released in 1946 cooperatively by the Agricultural Experiment Stations at Pullman, Washington; Moscow, Idaho; and Corvallis, Oregon. Despite the frequent use of cultivars, especially 'Bromar', it is probable that genetic variation exists in mountain brome associated with specific environments. Although relatively easy to establish, cultivars selected for vigor and pasture use may be maladapted to local environments, or they may be overly competitive, potentially leading to genetic swamping or difficulties in establishing mixed species plantings (Hufford and Mazer 2003). Thus, knowledge of the patterns of genetic variation across the landscape is needed to ensure that mountain brome germplasm used for restoration has long-term sustainability.

In this study, germplasm was collected from a wide range of environments in the Blue Mountains of northeastern Oregon and southeastern Washington, and evaluated in common-garden studies. The study objectives were (*i*) to link genetic variation in mountain brome traits to environments at seed source locations, (*ii*) to map the pattern of genetic variation in the Blue Mountains and create seed zones to delimit plant movement, and (*iii*) to compare Blue Mountain populations with other mountain brome germplasm, including 'Bromar'. This information will be used to develop an improved framework for guiding the collection, utilization, and management of mountain brome plant materials, especially for the Blue Mountains region.

Materials and methods

Plant materials

In 2002, wildland seed was collected from 193 mountain brome (*B. carinatus*) plants at 148 locations in the Blue Mountains of northeastern Oregon and southeastern Washington (Fig. 1). At 45 of the source locations, seeds were collected from two parent plants at the same elevation (a.s.l.) and site conditions, but separated by a minimum of 5 m to minimize potential relatedness of adjacent plants. All seed from an individual parent plant constituted a family. The purpose of including two plants from a subset of the source locations was to provide a pooled estimate of the variance among families-within-locations. The estimate was used as the error term in tests of significance of plant traits across seed source locations, and also for testing lack of fit in regression models.

For comparative purposes, seeds from an additional nine source locations in the Cascade Mountains of western Oregon were also included in the study, as were two accessions of 'Bromar' (Law and Schwendiman 1946). 'Bromar' accessions were obtained from germplasm collections at the

Fig. 1. Geographic variation for principal components (PC 1 and PC 2) for mountain brome (*Bromus carinatus*) within National Forest Boundaries of the Blue Mountains of northeast Oregon and southeast Washington. The maps are based on regression of PC 1 and PC 2 with environmental variables (see Table 6). Mean values are shown as the zero contours between yellow and light green. The contours intervals were based on an LSD at $P = 0.3$.

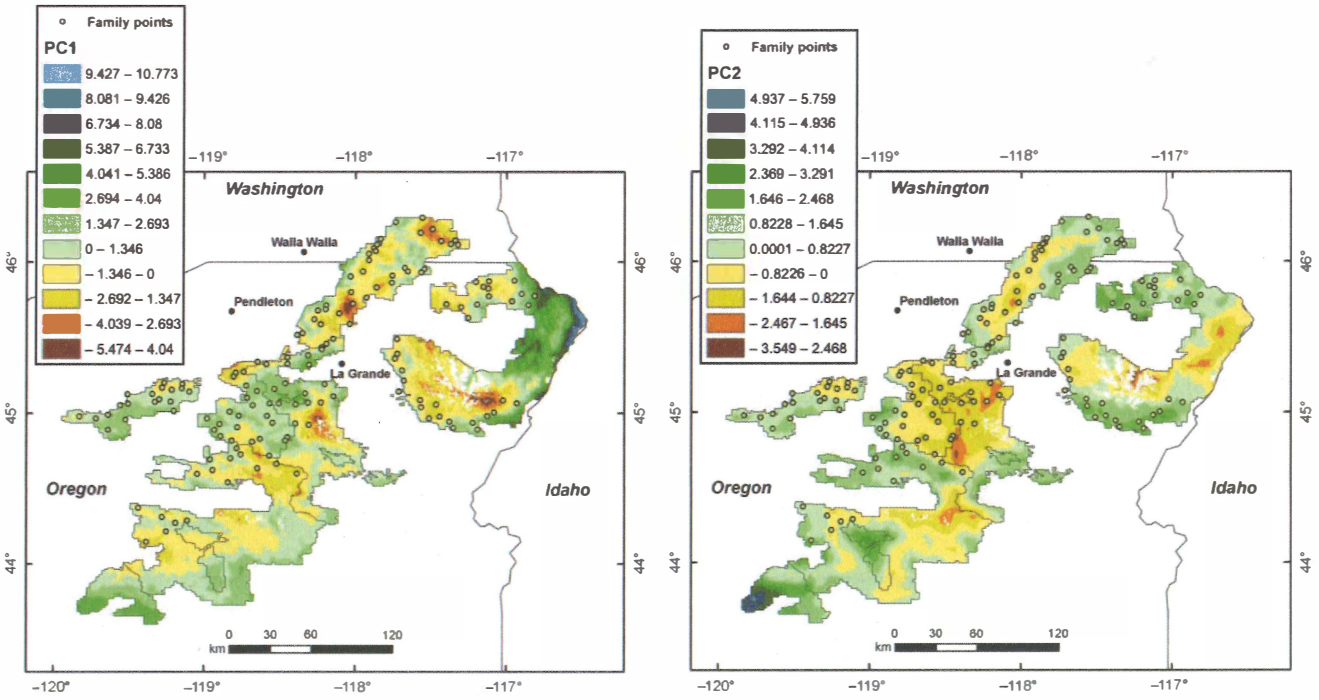

Table 1. Measured and derived plant traits for mountain brome (*Bromus carinatus*) and their descriptions taken in the spring and summer of 2004 and 2005 at Central Ferry and Pullman, Washington.

Trait	Abbreviation	Description
Date of first heading	Hd	Day of year when first inflorescence extends from sheath
Date of first anthesis	Blm	Day of year when anthers first appeared on inflorescences
Plant habit	PltHab	Rated from 1 = prostate to 9 = upright after heading
Leaf width*	LfWd	Width of an upper, fully emerged leaf (cm)
Leaf length*	LfLn	Length of an upper, fully emerged leaf (cm)
Leaf width to length ratio*	LfWdLn	Derived from leaf width and length data
Leaf color*	LfCol	Color of an upper, fully emerged leaf rated from 1 = light green to 9 = dark green
Leaf pubescence*	LfPub	On an upper, fully emerged leaf rated from 1 = no pubescence to 9 = heavy pubescence
Leaf texture	LfTex	Rated from 1 = coarse to 9 = fine on the entire plant before anthesis
Leaf texture to color ratio	LfTexCol	Derived from leaf texture and color ratings
Leaf abundance	LfAb	Leafiness at heading rated from 1 = low to 9 = high
Head abundance	HdAb	Relative density of inflorescences per plant rated from 1 = no heads to 9 = high head production
Plant height	Ht	From soil surface to upper plant after anthesis (cm)
Dry mass	None	Above ground plant dry mass cut at about 5 cm above ground at seed maturity (g)
Crown diameter	Diam	Measured perpendicular to rows after plants were cut for dry matter (cm)
Dry mass to plant height ratio	WtHt	Derived from aerial dry mass and plant height data
Dry mass to crown diameter ratio	WtDiam	Derived from aerial dry mass and crown diameter data

*Leaf width, length, color, and pubescence were measured on the same leaf for a given plant before anthesis.

United States Department of Agriculture – Natural Resource Conservation Service Plant Materials Center and the Western Regional Plant Introduction Station, both in Pullman, Wash.

At each wildland seed source location, elevation (a.s.l.), latitude, and longitude were obtained from geographic positioning instrumentation. Climate data were derived from PRISM spatial models at a resolution of approximately

4 km × 4 km raster cell size, using averages from 30 years (1961–1990) (Daly et al. 1994; www.ocs.orst.edu/prism). Climate values for the source locations were obtained using the LATTICESPOT function in ArcInfo Workstation 8.1 (ESRI 2008*a*) Climatic variables included monthly, seasonal, and annual minimum, maximum, and average temperatures at each collection source location; monthly and annual precipitation; the date of 50% probability of the last spring frost, first autumn frost, and the frost-free period; and the Martonne aridity index (De Martonne 1926). The Martonne index was calculated as [precipitation (mm)/(°C + 10)] using mean annual precipitation and temperature values. For 107 Blue Mountain source locations (138 families), soils data were available for a number of variables, including cation exchange capacity, bulk density, clay content, water holding capacity from 0–58 cm, organic matter from 0–2.5 cm depth, organic matter from 2.5–58 cm depth, pH from 0–5 cm depth, and pH from 5–58 cm depth. Soil attributes were determined from digital soil maps (1:24 000) and data generated by the Soil Data Viewer extension of ArcMap (soildataviewer.nrcs.usda.gov). The soil maps were developed following protocols of Winthers et al. (2005).

Experimental design

The common-garden experiments were established at the Central Ferry Research Farm (CF) (46°40′9″N, 117°45′21″W) and at the Pullman Plant Materials Center (PU) (46°43′9″N, 117°8′29″W), both in Washington State. Central Ferry is located in the Snake River Canyon at about 200 m a.s.l. Pullman is approximately 50 km east of CF at about 750 m a.s.l. Corresponding to its lower elevation (a.s.l.), temperatures at CF average about 3.5 °C higher than at PU. Precipitation averages 540 mm annually at PU and 350 mm at CF. Each experimental unit consisted of two plants from each family planted in three replications. These were randomized in complete blocks at both the PU and CF field sites. The experiment was conducted at two test sites and two years to evaluate interactions of traits with years and sites, and as such, to improve the probability of finding traits within years and sites with demonstrated genetic variation that may be associated with environmental factors at source locations. The PU and CF test sites were located approximately 60 and 45 km north of the Blue Mountains, respectively.

In July 2003, seeds were sown in germination boxes (13.3 cm long × 12.7 cm wide × 3.5 cm deep) containing water-saturated vermiculite. The boxes were placed at room temperature and seeds allowed to germinate on benches under laboratory conditions (~20 °C). The resulting seedlings were planted into "books" with five 2.5 cm^2 × 11.4 cm long plastic cells (Spencer-Lemaire Industries, Edmonton, Alberta, Canada) filled with potting soil (organic plug mix No. 5, Sungro Horticulture, Vancouver, British Columbia, Canada) and placed in trays. Each book was planted with the two seedlings representing one replication of each family. The plants were placed in trays and maintained outside during the summer of 2003, and watered and fertilized as needed to promote optimal growth.

Prior to transplanting, fields were cultivated to provide a suitable seed bed. Soil moisture at PU was excellent. At CF, dry soil conditions necessitated an initial irrigation of approximately 40 mm over the plot area prior to transplanting. On 17 September 2003 at PU and on 30 September 2003 at CF, transplanting was completed using a Model 900 Mulch Transplanter (Mechanical Transplanter Co., Holland, Michigan, USA) modified to accommodate the 2.5 cm^2 × 11.4 cm plant plugs. Plants were spaced 0.6 m apart within rows and rows were spaced 2.1 m apart. At the PU site, fertilizer was applied at a rate of 112 $kg \cdot ha^{-1}$ nitrogen and 34 $kg \cdot ha^{-1}$ sulfur on 27 October 2003. On 13 October 2004 an application was completed at half the rates for 2003. At CF, 67 $kg \cdot ha^{-1}$ of nitrogen was applied prior to transplanting, with no additional fertilizer added after transplanting. Soil tests suggested that adequate P and K were available.

Statistical analysis

The general statistical methodology followed the procedures of Campbell (1986) for describing and mapping genetic variation in conifer species. This process involves collection of plant material from a large number of locations and analysis of numerous plant traits describing phenology, morphology, and production in common-garden experiments (Table 1). Traits with strong genetic variation among source locations are selected for principal component (PC) analysis to reduce the number of traits to a smaller set of orthogonal variables. The PC scores, as composite plant traits, are then regressed on environmental variables to derive models for mapping seed zones. In this approach, genetic differences associated with seed source environment are assumed to arise through local selection pressures and are therefore adaptive (Morgenstern 1996).

Trait measurements at both test sites were taken in the spring and summer of 2004 and 2005. Analyses of variance were conducted on plot means for each trait and year of measurement. The general linear models procedure (PROC GLM) from SAS (SAS Institute Inc. 1999) was used to partition the variation into test site, blocks within sites, seed source locations, families within source locations, and associated interactions. The error term for testing sites (CF and PU) was the block within site variance. The error for testing seed source locations was the family within source location variance, and the error for testing the site × source location interaction was the site × family within source location interaction. Source locations, families and blocks were all considered random effects; common garden test sites were considered fixed.

The protocol for selection of plant traits used for principal component analysis was designed to ensure traits represented genetic variation with minimal redundancy. Only variables with significant ($P < 0.05$) seed source location effects or seed source location × site interactions, were considered for regression analysis. If a trait within a year and common-garden site was correlated with another trait at $r \geq 0.8$ using Pearson's coefficient, it was considered redundant and only data from one of the traits was used in further analyses. In addition, we wanted to ensure there was no functional duplication of traits between sites, so only when the site × source location interaction was significant for a given trait ($P < 0.05$) and the Burdon correlation (Burdon 1977) between sites was less than 0.75, were the same traits from different garden sites included as distinct variables for principal component analyses. The between Burdon site cor-

relation was calculated as the source location variance from both sites divided by the sum of the source location and source location × site variance at both sites. If a trait was determined to be redundant using the above protocol, a single trait was used by selecting the CF, PU, or combined site mean. This was done by selecting the effect with the largest *F*-ratio. And finally, the Q_{st}, which is the proportion of genetic variation among source locations relative to the total of among plus within variation (McKay and Latta 2002), was used to further evaluate and reduce the number of traits. To ensure that a high fraction of the variation was among source locations, a Q_{st} of at least 0.40 was required to retain a given trait for the final analysis.

Principal components (PCs) were computed through analysis of the trait correlation matrix using SAS (PRINCOMP) (SAS Institute Inc. 1999). Principal component scores were calculated for each family using the eigenvectors from the first five principal components. The R^2 regression option in SAS (PROC REG) was then used to relate PC scores to selected environmental variables at seed source locations. This involved including various combinations of environmental variables in preliminary models using the R^2 option. The Akaike's information criterion (AIC) and the Sawa's Bayesian information criterion (BIC) were also determined in PROC REG. A high R^2 with a low AIC and BIC maximizes the fit and omits variables that increase the R^2 but do not truly improve the model (SAS Institute Inc. 1999). The final PC 1 and PC 2 regression models were selected to have the highest R^2 at the lowest AIC and BIC values possible.

The models relating PC's with environmental variables were tested for lack of fit using the families within source location variance as the error term. Lack of fit is caused by source location variation that is not explained by the selected model. For the lack of fit analysis, the sums of squares for each parameter in the model was summed and divided by the total sums of squares. The total sums of squares included the portion from the model parameters plus the residual for locations. Thus, the model variability relative to the total gave the proportion of variability explained by the model; that is, the model R^2.

Trait means of plants originating in the Blue Mountains were compared with the means of 'Bromar' and those from the Western Cascades sources. For locations with more than one family at a given location, data were averaged. Then data from all locations in the Blue Mountains and the Western Cascades, along with 'Bromar', were used in analyses of variation for each trait. The resulting residual mean square error was used to calculate LSD values at $P < 0.05$ for determining differences between the Blue Mountains, Western Cascades, and 'Bromar' groups. In addition, each source location mean for a given trait was standardized to a mean of zero and a variance of one, and a matrix developed based on Euclidian distance. The first and second principal component values from the distance matrix were calculated and plotted using NTSYSpc software (Exeter Software, Setauket, New York).

Mapping and seed zone delineation procedures

Spatial mapping of PC values predicted from the final regression model was completed using the grid algebra function (Raster Calculator) of the ArcGIS 9.3 Spatial Analyst extension (ESRI 2008*b*) by multiplying each environmental variable by the respective regression coefficient and summing the results. The 4 km climate data were resampled to 800 m resolution to smooth out the resulting maps. Map boundaries were limited to sampled portions of the Ochoco, Umatilla, and Wallowa–Whitman National forests, including private in-holdings. Within these boundaries, mapping was completed only for areas below 2285 m a.s.l., above which no samples were collected. The total mapped area was approximately 2.23 million ha. The derived genetic map describes the overall pattern of genetic variation in the Blue Mountains as predicted by the environment. Seed zones delineating similar genetic types in the Blue Mountains were created by first classifying each PC raster into high and low categories centered at zero, and then overlaying the resulting rasters, similar to St Clair et al. (2005). Similar to the methods of Rehfeldt (1986), a contour interval corresponding to an $LSD_{0.3}$ was calculated based on the error derived from replication of families within source locations. The spatial combination (overlays) of PC 1 and PC 2, each with two zones, resulted in four seed zones combining attributes of both PCs.

Results

Genetic variation among seed source locations

In 2004, all but 5 of the 17 measured traits in Table 1 showed significant source location genetic variation at CF, PU, or both sites (data not shown) ($P < 0.05$). Variables not significant in 2004 included head abundance, leaf abundance, leaf texture, leaf texture:color ratio, and leaf width:length ratio. The site × source location interactions for those variables were also not significant ($P < 0.05$). As a result, those 2004 variables were eliminated as plant traits for the PC analysis. In 2005, genetic variation for source locations was significant ($P < 0.05$) for all traits except bloom date, leaf width:length ratio, plant height, and mass:diameter ratio, so those traits were also eliminated. For the remaining traits, results for each year and site combination were examined as described above and 16 final traits selected (Table 2) for use in the PC analysis.

Relationship of traits with seed source environment

Of the 53 climate variables generated by the PRISM model for each source location, the strongest correlations with measured plant traits tended to involve both monthly and annual temperature minimums, maximums, averages, as well as precipitation and frost patterns. In general, the same pattern of correlation was observed for monthly temperature and precipitation as for correlations based on annual data. For example, head abundance (HdAb05) was correlated with monthly precipitation for 11 of 12 months and also with annual precipitation (Table 3); on the other hand, neither monthly nor annual precipitation were correlated with leaf width (LfWd05CF). Since no obvious monthly patterns were detected, the annual temperature and precipitation variables were used to summarize the correlation results (Table 3).

The majority of the correlations between plant traits and environmental variables were significant at $P < 0.01$, with certain traits tending to be more frequently associated with

Table 2. Results of analyses of variance for selected traits from 148 mountain brome (*Bromus carinatus*) seed source locations (Loc) collected from the Blue Mountains of Oregon and Washington State, USA, and measured in common-garden experiments at Central Ferry (CF) and Pullman (PU) Washington in 2004 and 2005.

Trait*	Loc min.-max.	Loc mean	Loc mean square	*F* value‡	*P* value
Hd05PU	116 to 144 d	132.00	106.6	2.61	<0.001
PltHab04PU	1.3 to 9.0†	5.61	9.279	2.52	<0.001
PltHab05PU	1.3 to 9.0†	5.59	5.104	2.55	<0.001
LfWd05CF	0.6 to 1.4 cm	0.99	0.0395	2.32	0.001
LfLn05	15.4 to 30.3 cm	21.90	30.18	2.54	<0.001
LfPub04CF	1.0 to 9.0†	3.89	18.56	4.00	<0.001
LfPub05	0.8 to 9.0†	5.41	20.05	4.22	<0.001
LfAb05CF	1.0 to 8.7†	4.36	6.403	2.22	0.001
HdAb05	3.3 to 6.8†	4.98	1.392	1.74	0.016
Diam04PU	9.7 to 22.3 cm	14.83	22.22	2.07	0.003
Diam05CF	7.1 to 42.7 cm	21.59	105.8	1.90	0.007
Diam05PU	16.3 to 48.2 cm	28.76	122.9	2.80	<0.001
WtHt04PU	0.6 to 3.7 $g \cdot cm^{-1}$	1.77	1.108	2.79	<0.001
WtHt05	2.0 to 9.4 $g \cdot cm^{-1}$	4.55	5.445	1.99	0.004
WtDiam04CF	3.5 to 18.7 $g \cdot cm^{-1}$	9.23	26.09	2.13	0.002
WtDiam04PU	2.6 to 17.0 $g \cdot cm^{-1}$	8.85	23.55	2.42	<0.001
Prin1	–4.7 to 6.8	0.00	5.25	3.26	<0.001
Prin2	–4.1 to 3.8	0.00	2.97	4.83	<0.001

*See Table 1 for trait codes.

†Rated from 1 (prostrate habit, no leaf pubescence, low leaf or head abundance) to 9 (upright habit, heavy leaf pubescence, high leaf or head abundance).

‡Using the variance for families among locations (df = 147) tested with the variance for family within location as the error term (df = 45).

the environmental variables (Table 3). For example, the mass:height ratio (WtHt05) was significantly correlated with all 11 environmental factors, leaf length (LfLn05) with 10 of 11, and mass:diameter ratio (WtDiam04CF) with 9 of 11 factors (Table 3).

For traits with a dry mass component (mass:diameter and mass:height ratios) correlations were negative for precipitation and elevation (a.s.l.) and positive for annual and maximum temperature (Table 3). This was also true for dry mass per se, which correlated with precipitation (r = –0.27), elevation a.s.l. (r = –0.34), spring frost date (r = –0.23), average temperature (r = 0.32), and maximum temperature (r = 0.32) ($P < 0.01$, n = 193). Thus, higher dry matter production was associated with source locations that had higher temperatures, less precipitation, and lower elevations (a.s.l.)

Heading date (Hd05PU), the only selected trait directly related to plant phenology, was correlated positively with average and maximum temperature, and negatively with elevation (Table 3). Leaf length (LfLn05) and leaf pubescence (LfPub04CF and LfPub05) were positively correlated with minimum temperature, first fall frost date and the frost free period, and negatively correlated with last spring frost date. Thus, source locations with higher minimum temperatures and longer frost free periods generally had longer, more pubescent leaves (Table 3).

The most frequent correlations with soil factors were observed with the percentage of clay and pH variables (Table 3). Except for the mass:height ratio (WtHt04PU), traits with a dry mass component correlated positively with percentage of clay, pH from 0–5 cm depth, and pH from 5–56 cm depth. Across source locations, the clay fraction averaged 16.4% and ranged from 3% to 36%. The sand fraction averaged 33% but ranged from 20% to 90%, and the silt fraction averaged 52%, ranging from 7% to 68% (data not shown). Thus, soil texture across source locations had relatively low clay fractions consistent with the sandy, silty, and loamy soils that dominate the Blue Mountains region. Those soils are typical of mountain brome habitat, yet the clay fraction was the texture variable most frequently and strongly correlated with measured plant traits.

Principal components, individual traits, and seed source environments

The first two principal components explained 42.6% of the variance in the 16 selected traits (Table 4). Principal components 3, 4, and 5 explained only an additional 9.7%, 9.3%, and 6.8% of the source location variance, respectively (data not shown). Given the relatively small variation explained by PC's beyond the first two, and the asymptotic decline, only the first two components were used in subsequent regression modeling with seed source environmental variables.

The loading factors for PC1 were frequently strong for plant traits associated with production (i.e., leaf and head abundance, crown diameter, and plant mass:height ratios, Table 4), which all correlated with dry matter ($P < 0.05$, n = 193). The PC 1 loading for heading date (Hd05PU) was also relatively high, indicating that delayed floral development contributed to higher PC 1 scores. There was a contrast between PC 1 and PC 2 for Diam04PU with PC 1 loading for relatively high diameter and for PC 2 for relatively low diameter. Strong loadings for PC 2 were most fre-

Table 3. Correlations of selected plant traits from common-garden experiments at Pullman (PU) and Central Ferry (CF) Washington, USA, in 2004 (04) and 2005 (05) with environmental variables from mountain brome (*Bromus carinatus*) seed source locations the Blue Mountains.

Trait*	Mean annual precipitation (mm)	Mean annual temp. (°C)	Min. annual temp.	Max. annual temp.	Date of first fall frost	Date of last spring frost	Days frost free	Elevation (m a.s.l.)	Percentage of clay	pH at depth 0–5 cm	pH at depth 5–56 cm
Hd05PU	ns	0.243**	ns	0.302**	ns	ns	ns	–0.293**	ns	ns	ns
PltHab04PU	ns	ns	ns	0.227**	ns	ns	ns	ns	0.181*	ns	ns
PltHab05PU	ns	ns	–0.185*	ns	ns	ns	ns	ns	0.171*	ns	0.209*
LfWd05CF	ns	ns	0.167*	ns	ns	ns	ns	ns	ns	ns	ns
LfLn05	–0.169*	0.329**	0.158*	0.317**	0.300**	–0.286**	0.298**	–0.375**	0.253**	ns	0.254**
LfPub04CF	0.149*	ns	0.211**	ns	0.214**	–0.257**	0.242**	ns	ns	ns	ns
LfPub05	ns	ns	0.247**	–0.148*	0.228**	–0.247**	0.243**	ns	ns	ns	ns
LfAb05CF	–0.165*	ns	ns	ns	ns	ns	ns	ns	ns	ns	0.219*
HdAb05	–0.202**	0.159*	ns	0.234**	ns	–0.152*	ns	–0.170*	ns	0.197*	0.281**
Diam04PU	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Diam05CF	ns	0.165*	ns	0.175*	0.146*	–0.161*	0.157*	–0.148*	ns	0.221**	ns
Diam05PU	ns	0.149*	ns	0.190**	0.297**	–0.276**	0.291**	–0.241**	ns	ns	ns
WtHt04PU	–0.333**	0.153*	ns	0.201**	ns	ns	ns	–0.213**	ns	ns	ns
WtHt05	–0.244**	0.317**	0.149*	0.309**	0.273**	–0.304**	0.295**	–0.351**	0.174*	0.257**	0.262**
WtDiam04CF	–0.276**	0.374**	0.182*	0.359**	ns	–0.160*	ns	–0.405**	0.193*	0.255**	0.354**
WtDiam04PU	–0.406**	0.272**	ns	0.396**	ns	ns	ns	–0.321**	0.210*	0.187*	0.216*
Mean	773	6.1	0.3	12.0	257	156	101	1479	16.4	6.1	6.5
Minimum	417	3.8	–3.1	8.9	238	140	55	750	3.0	5.0	5.6
Maximum	1587	8.2	3.4	14.7	273	184	130	2285	36.3	8.0	7.8

Note: *, $P < 0.05$; **, $P < 0.01$; ns, not significant. Data for precipitation, temperature, frost, and elevation (a.s.l.) were from $n = 193$ families and 148 source locations; data for clay and pH were from $n = 138$ families and 107 source locations.

*See Table 1 for trait codes and units of measurement.

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Table 4. Loading factors for principal components (PC 1 and PC 2) for selected plant traits measured on mountain brome (*Bromus carinatus*) from the Blue Mountains (n = 193 families from 148 source locations).

	Loading factors	
Trait*	PC 1†	PC 2†
Hd05PU	0.228	–0.119
PltHab04PU	–0.149	0.429
PltHab05PU	–0.049	0.195
LfWd05CF	–0.159	0.186
LfLn05	0.181	0.361
LfPub04CF	–0.024	–0.417
LfPub05	–0.068	–0.421
LfAb05CF	0.316	–0.084
HdAb05	0.376	0.065
Diam04PU	0.266	–0.217
Diam05CF	0.375	–0.112
Diam05PU	0.249	–0.003
WtHt04PU	0.315	–0.034
WtHt05	0.377	0.089
WtDiam04CF	0.295	0.199
WtDiam04PU	0.133	0.357

Note:
*See Table 1 for traits codes and measurement units.
†PC 1 explained 27.5% of the variation and PC 2 explained 15.1% for a total of 42.6%.

Table 5. Correlations between principal components (PC 1 and PC 2) and environmental variables at mountain brome (*Bromus carinatus*) seed source locations in the Blue Mountains.

	PC 1	PC 2
General environmental factors, n = 193		
Latitude	–0.11ns	–0.14ns
Longitude	–0.10ns	0.05ns
Elevation	–0.33**	–0.28**
Annual minimum temp.	0.06ns	–0.08ns
Annual maximum temp.	0.32**	0.3**
Annual average temp.	0.26**	0.17*
Annual average precip.	–0.31**	–0.23**
Martonne aridity index	–0.33**	–0.23**
Fall frost date	0.17*	–0.07ns
Spring frost date	–0.22**	0.06ns
Frost free days	0.20**	–0.07ns
Soil factors, n = 138		
Cation exchange capacity	0.01ns	0.17*
Bulk density	0.14ns	0.22**
Clay content	0.09ns	0.24**
Water holding capacity	–0.08ns	–0.21*
Organic matter 0–2.5 cm	–0.16ns	–0.19*
Organic matter 2.5–58 cm	–0.09ns	0.18*
pH 0–5 cm	0.22**	0.12ns
pH 5–58 cm	0.28**	0.24**

Note: *, $P < 0.05$; **, $P < 0.01$; ns, not significant. There were 193 families and 148 source locations for the general environmental factors and 138 families and 107 source locations for soil variables.

quently associated with morphological factors such as plant habit, leaf length, and leaf pubescence (Table 4). The strong loading of WtDiam04 PU for PC 2, a production trait, was the only notable exception to the association of PC 2 with morphological factors.

Similar to individual traits, correlations between PCs and environmental variables were observed with elevation (a.s.l.), annual and maximum temperature, precipitation, and frost patterns (Table 5). One exception was that neither PC 1 nor PC 2 was significantly correlated with annual minimum temperature. Correlations between PC 1 and environmental variables (Table 5) showed that higher PC 1 scores were more prevalent at source locations from lower precipitation areas with warmer environments typical of lower elevations. Except for the variables associated with frost, correlations of PC 2 were similar to those for PC 1.

There were also significant correlations between PC 1 and PC 2 and soil factors (Table 5). For PC 1, higher scores were associated with source locations with higher soil pH, which usually occurred at lower elevations. For PC 2, source locations with higher bulk density, higher clay content, lower water holding capacity, lower organic matter tended to produce plants with higher PC 2 values. Since soil data were not available for 41 of the 148 source locations, soil attributes were not considered in the regression modeling presented below. However, our results suggest that soil factors, often neglected in genecology studies, certainly have potential as important explanatory variables in seed zone modeling.

Regression models and mapped genetic variation

Regression modeling of PC 1 scores resulted in an 11-variable model that explained 46% of the source location variation (Table 6). For PC 2, regression modeling resulted in an 8-variable model that explained 40% of the source location variation. Although there was considerable residual error or lack of fit associated with both models, they were sufficiently strong to produce meaningful landscape maps of plant adaptation zones for the Blue Mountains (Figs. 1 and 2).

Maps of PC 1 and PC 2 graphically illustrated differences in genetic variation with environmental gradients (Fig. 1). The highest PC 1 and PC 2 values are shown in shades of blue and represent a low fraction of the total mapped area (Fig. 1). That was also true for the lowest PC 1 and PC 2 values (brown areas, Fig. 1), which mapped to the highest elevations (a.s.l.). The relatively low PC 1 regression values (yellow to orange hues) mapped to generally higher elevations with corresponding lower maximum temperatures and higher precipitation.

For PC 2, higher (yellow to orange hues) to lower (greener hues) regression values were often observed from lower to higher elevations, similar to PC 1 (Fig. 1). However, that was not always the case, as the area west of the Snake River bordering Idaho had relatively high PC 1 and lower PC 2 values. A similar pattern was observed in the area south of Pendleton, Oregon (centered approximately around –118.5°W and 45°N) with areas mapping for higher PC 1 (lighter green hues) and lower PC 2 values (yellow hues).

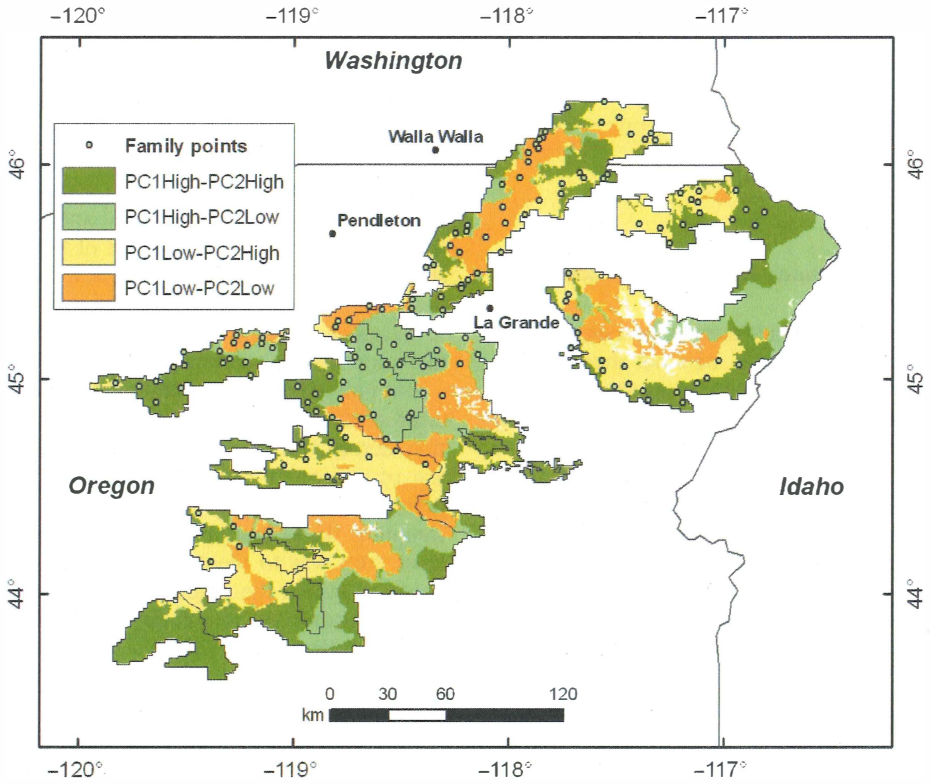
The spatial overlays of PC 1 and PC 2, each with two zones, resulted in four proposed seed zones combining at-

Table 6. Regression models showing coefficients, their *P* values, and regression fit (R^2) used for mapping principal components (PC 1 and PC 2) with environmental variables.

PC 1			PC 2		
Variable*	Regression coefficient	Coefficient *P*-value	Variable*	Regression coefficient	Coefficient *P* value
Intercept	315.8	<0.001	Intercept	–1.8158	0.412
Latitude	–3.1948	<0.001	Mxt Aug	0.7235	<0.001
Longitude	1.6291	<0.001	Mxt Sept	–0.8483	<0.0001
Elevation	–0.0022	0.002	Precip May	0.0642	<0.0001
Mxt Jan	0.9647	0.008	Aridity June	–2.2249	<0.0001
Mxt Feb	–1.2611	<0.001	Mnt April	–0.5325	0.006
Mxt April	1.4796	<0.001	Mnt Nov	1.1237	0.0058
Mxt July	–1.5709	<0.001	Mnt Dec	–0.9128	0.0149
Mxt Sept	0.9416	<0.001	Model fit $R^{2\dagger}$	—	40%
Precip Oct	0.1225	<0.001			
Precip Dec	–0.0635	<0.001			
Fall frost date	0.1268	<0.001			
Model fit $R^{2\dagger}$	—	46%			

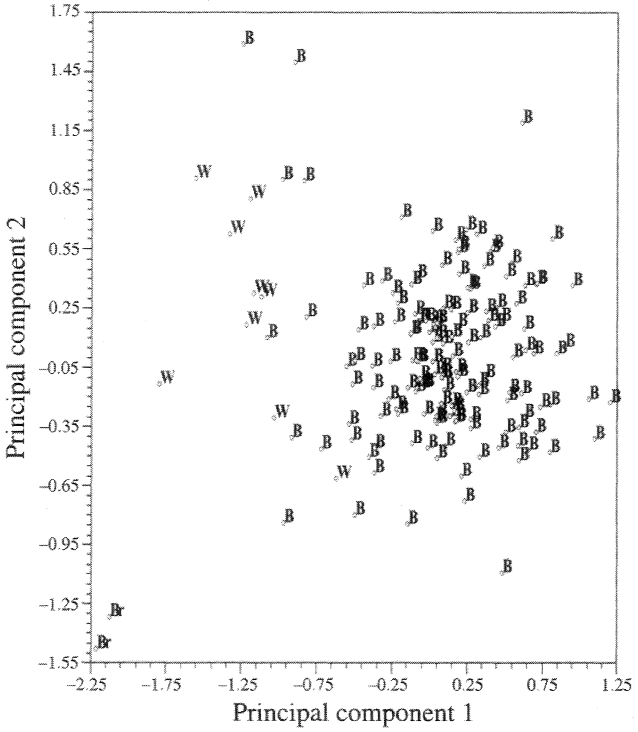
*Mxt, maximum temperature; Mnt, minimum temperature; aridity is the Martonne index.
†Calculated as the fraction of variability explained by the model relative to the total, which is the model plus residual source location variation.

Fig. 2. Proposed seed zones derived from overlaying principal components (PC 1 and PC 2) for mountain brome (*Bromus carinatus*) within National Forest boundaries of the Blue Mountains of northeast Oregon and southeast Washington.



tributes of both PCs (Fig. 2). This allowed visualization of areas of genetic variation in relation to environment using both PC 1 and PC 2 trait information. The four combinations of PC 1 and PC 2 show areas where different plant types would be expected. For example, the dark green areas (high PC 1 and high PC 2) would be expected to have plants with generally higher growth potential, more upright habit, longer leaves, dense foliage and less pubescence (Fig. 2). The combination of low PC 1 and low PC 2, mapped to orange, represented areas were plants would be expected to have lower growth potential with more prostrate habit, shorter leaves, and less pubescence.

Fig. 3. Principal component (PC 1 and 2) scores based on plant traits taken in common garden test sites at Pullman and Central Ferry, Washington, USA, for mountain brome (*Bromus carinatus*) germplasm from the Blue Mountains (B) (n = 146) of southeast Washington and northeast Oregon, the Western Cascades of Oregon (W) (n = 9), and the cultivar 'Bromar' (Br) (n = 2).



Comparisons of Blue Mountains, Western Cascades, and 'Bromar' seed sources

'Bromar' differed from the Blue Mountains sources in 15 of 18 plant traits compared ($P < 0.05$, data not shown). This included all traits in Table 3 plus dry mass for 2004 and 2005. Only plant habit traits (PltHab04 and 05) and leaf width (LfWd05CF) did not differ. 'Bromar' had greater crown diameter, later heading, more seed heads, more leaves, longer leaves, less pubescence, and higher plant dry mass than the mean of the Blue Mountains group. Most striking were differences in head and leaf abundance and all traits associated with dry mass. For example, head abundance (HdAb05) was 70% higher for 'Bromar' than the Blue Mountains group, and 90% higher for leaf abundance (LfAb05CF). 'Bromar' dry mass was 2.6 times higher in 2004 and 3.8 times higher in 2005 than the Blue Mountains group.

'Bromar' was more comparable with sources from the Western Oregon Cascades than the Blue Mountains, but Cascade sources still differed for 11 of the 18 traits ($P < 0.05$, data not shown). Not differing were heading, leaf length, and crown diameter traits. Plant traits with a dry mass component were always higher for 'Bromar' than the Western Oregon Cascades group, with the Cascades group intermediate between the Blue Mountains and 'Bromar' sources. Plots of multivariate trait scores (PC 1 and PC 2) for mountain brome from the Blue Mountains, the Western Cascades, and 'Bromar' sources showed results similar to the individual traits comparisons. Although there was some overlap between the Blue Mountains and the Western Cascades sources, the 'Bromar' sources were completely distinguished from the other two groups (Fig. 3).

Discussion

Statistical approach

In this approach to genecology we assumed there was adequate sampling of source locations across the mapped area, and that local plant material was optimally adapted to a given location (Campbell 1986). Thus, the experimental design put a premium on including a large number of different source locations to ensure adequate sampling across the landscape for regression modeling. This was balanced against having a smaller number of families within source locations for calculating the error term to test genetic variation among traits. Since the subset of locations with two families was randomly and spatially distributed across the Blue Mountains study area, and the degrees of freedom were relatively high, we believe it resulted in a valid estimate of family-within-location variance, even though duplicate families were not sampled at all locations. This approach has been used successfully in numerous studies, including Ager et al. (1993) for red alder (*Alnus rubra* Bong.), Erickson et al. (2004) for blue wildrye, and St Clair et al. (2005) for Douglas fir (*Pseudotsuga menziesii* (Mirb.) Fronco var. *menziesii*). A traditional analysis of variance uses the residual variance associated with the block × source location as the error term, and would include families from all locations. We conducted analyses of variation using that approach, and found that all of the traits in Table 1 had strong location effects ($P < 0.0001$). So whether using families-within-locations or the variance associated with blocks × locations as error terms, there was unequivocal evidence that source locations varied across the Blue Mountains.

But unlike blocks × locations, the families-within-location error term directly tests for source-location genetic variation across the landscape (Campbell 1986), which is the test of interest in genecology studies. Rather than for comparing location means, which would likely warrant more sampling, the primary purpose of the families-within-location error term was to identify traits that showed genetic differentiation across the landscape. This guided the selection of genetic traits used in principal component analysis, regression modeling, and mapping. Since the correlation analysis showed strong associations between individual and composite (PC 1 and PC 2) plant traits and environmental variables (temperature, precipitation, and frost patterns) (Tables 3 and 5), and the regression models explained a reasonably high proportion of the variation (Table 6), it appeared that the methodology was successful.

The significant residual error or lack of fit in regression models, however, leaves room for other factors to influence patterns of genetic variation in mountain brome in the Blue Mountains. Those factors, among other things, could include microclimates, biotic interactions, soil factors, and degrees of adaptive plasticity in situ (Kawecki and Ebert 2004).

Genetic variation and adaptation

Since the main purpose of this research was to provide guidance for mountain brome restoration in the Blue Mountains on a scale impractical for a reciprocal transplant study, the common-garden approach was used. As such, a direct test of natural selection for local adaptation was not possible (Kawecki and Ebert 2004). However, there was evidence that our assumption of adaption was reasonable. Genetic variation in traits was linked with environmental variables through correlations (Table 3) that are logical with respect to temperature and precipitation gradients (Fig. 1). For example, plants at locations with higher temperatures appeared genetically disposed to fit environments with longer growing seasons, more moderate precipitation, and the potential for greater dry matter accumulation typical of lower elevations. Moreover, later heading associated with higher temperature environments at lower elevations (a.s.l.) was consistent with genetic differences in phenology fitting the environment. The later heading results in more time for leaf and tiller growth and development and thus more dry mass accumulation before anthesis. At higher elevations (a.s.l.), earlier heading fits an environment with much cooler temperatures and a shorter growing season. Certainly it would be unlikely that plants adapted to the warmer temperatures, lower precipitation, and later development environments typical of lower elevation locations in the Blue Mountains would be well adapted to the colder and wetter conditions at higher elevations.

Seed transfer zones

Other genecology studies linking genetic variation to environmental variables to develop seed transfer zones have generally involved commercially important conifer species (Campbell 1986; Rehfeldt 1994; Johnson et al. 2004; St Clair et al. 2005). Those studies showed that the size and scope of adaptation zones were species dependent, precluding generalized seed zones. Since there are few genecology studies of native perennial grasses, it is not yet clear if similar patterns of species specific adaptation can be expected. In a study similar to ours, Erickson et al. (2004) found that blue wildrye (*Elymus glaucus* Buckley) in the Blue Mountains was associated with longitude and Omernik level 4 ecoregions (Omernik 1987). Blue wildrye seed transfer zones were divided into western and eastern sections delimited at 118°45′W. We tested for differences in mountain brome between PC 1 and PC 2 means east and west of that longitude and found no significant difference ($P < 0.05$). Since our results did not parallel those of Erickson et al. (2004), species specificity for seed zones was indicated.

Means of PC 1 and PC 2 derived from the nine Omernik level 4 ecoregions in our mountain brome study area did show significant differences suggesting a link between ecoregion and genetic variation (data not shown). However, analysis of covariance showed most of the variation associated with ecoregions was also explained by elevation. Although ecoregions can provide useful categorical information for seed transfer, we did not find them a surrogate for the mountain brome seed zones in this study.

Conclusions and recommendations

The results suggest that the best option for restoration of mountain brome in the Blue Mountains is to collect and utilize seeds following the seed zone delineations in Fig. 2. The seed zones are relatively contiguous and manageable, and their utilization in restoration ensures that plant materials within zones will likely be suited to prevailing environmental conditions. This approach would leave open the prospect for natural selection of populations to specific micro-environments within the seed zones. This is similar to the "coarsely adapted" genetic mixtures described by McKay et al. (2005). The contrasts between 'Bromar' and plants from the Blue Mountains and Western Cascades of Oregon showed 'Bromar' to have unusually high and vigorous growth. To the extent that it is more competitive, extensive use of 'Bromar' for restoration could lead to genetic erosion within local populations of mountain brome, as well as displace other species and reduce the overall diversity of restored plant communities. As a result, the utilization of 'Bromar' for revegetation in this region should be carefully considered.

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