Communications

Ecological Applications, 24(5), 2014, pp. 913–919

Generalized provisional seed zones for native plants

Andrew D. Bower,[1,4] J. Bradley St. Clair,[2] and Vicky Erickson[3]

[1]*USDA Forest Service, Olympic National Forest, 1835 Black Lake Boulevard SW, Olympia, Washington 98512 USA*
[2]*USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, Oregon 97330 USA*
[3]*USDA Forest Service, 1220 SW 3rd Avenue, Portland, Oregon 97204 USA*

Abstract. Deploying well-adapted and ecologically appropriate plant materials is a core component of successful restoration projects. We have developed generalized provisional seed zones that can be applied to any plant species in the United States to help guide seed movement. These seed zones are based on the intersection of high-resolution climatic data for winter minimum temperature and aridity (as measured by annual heat : moisture index), each classified into discrete bands. This results in the delineation of 64 provisional seed zones for the continental United States. These zones represent areas of relative climatic similarity, and movement of seed within these zones should help to minimize maladaptation. Superimposing Omernik's level III ecoregions over these seed zones distinguishes areas that are similar climatically yet different ecologically. A quantitative comparison of provisional seed zones with level III ecoregions and provisional seed zones within ecoregions for three species showed that provisional seed zone within ecoregion often explained the greatest proportion of variation in a suite of traits potentially related to plant fitness. These provisional seed zones can be considered a starting point for guidelines for seed transfer, and should be utilized in conjunction with appropriate species-specific information as well as local knowledge of microsite differences.

Key words: adaptive traits; aridity; ecoregion; genetic variation; local adaptation; native plants; precipitation; restoration; seed transfer guideline; seed zone; temperature.

Introduction

The use of native plant species in ecological restoration has become increasingly prevalent in the United States, particularly on western federal lands, and is expected to increase in the future due to challenges such as climate change, severe wildfires, invasive plants, and declining populations of at-risk species (USDA Forest Service 2012*a*). The introduction of novel and potentially maladapted genotypes is a major concern in restoration. Nonlocal genotypes may reduce the success of restoration projects if they are maladapted, and could negatively affect adjacent native populations adapted to local environmental conditions through gene flow (McKay et al. 2005). Restoration with native plants is still relatively new in the western United States and the supporting research, infrastructure and plant material development programs are all in early stages of development (Erickson 2008, Johnson et al. 2010*a*, USDA Forest Service 2012*b*). Several United States federal and state agencies either suggest or require the use of locally adapted and regionally appropriate native plant materials based on site characteristics and ecological setting (see Appendix 1 in Johnson et al. 2010*a*). This means that plant germplasm should be adapted to current environments, yet also possess sufficient diversity to adapt and respond to ever-changing biotic and abiotic conditions. However, sufficient information on plant responses to key environmental gradients such as temperature and precipitation is lacking for the vast majority of native grasses, forbs, and shrubs used in restoration.

Results from genetic studies of forest trees show that adaptive variation is often associated with seasonal temperature and moisture regimes of the source environment (e.g., temperature, precipitation, number of frost free days, drought indices, etc. [Aitken et al. 2008, Chimura et al. 2011]). Patterns of genetic variation vary greatly among species. Some are climatic specialists that exhibit strong differentiation over small geographic scales, and thus, should not be moved far into different

Manuscript received 11 February 2013; revised 3 February 2014; accepted 12 February 2014. Corresponding Editor: E. A. Leger.
[4] E-mail: abower@fs.fed.us

TABLE 1. Empirical seed zone delineation based on U.S. Government agency common garden tests of important restoration species of native plants other than trees.

Species	Source	Principals	Current status†
Blue wildrye (*Elymus glaucus* Buckley)	e. OR, n. CA	R6, PNWRS	Erickson et al. (2004)
Broadleaf lupine (*Lupinus latifolius* Lindl. ex J. Agardh)	w. OR, WA	R6	Doede (2005)
Oceanspray (*Holodiscus discolor* (Pursh) Maxim.)	w. OR, WA	NRCS, PNWRS	Horning et al. (2008)
Roemer's fescue (*Festuca idahoensis* Elmer ssp. Roemeri (Pavlick) S. Aiken)	w. OR, WA	NRCS, PNWRS	Wilson et al. (2008)
California brome (*Bromus carinatus* Hook and Arn,)	e. OR, e. WA	R6, ARS	Johnson et al. (2010*b*)
Bigleaf lupine (*Lupinus polyphyllus* var. *polyphyllus*)	w. OR	IAE, NRCS	Miller et al. (2011)
Wooly sunflower (*Eriophyllum lanatum* var. *leucophyllum*)	w. OR	IAE, NRCS	Miller et al. (2011)
Denseflower willowherb (*Epilobium densiflorum*)	w. OR	IAE, NRCS	Miller et al. (2011)
Slender cinquefoil (*Potentilla gracilis* var. *gracilis*)	w. OR	IAE, NRCS	Miller et al. (2011)
Oregon saxifrage (*Saxifraga oregano*)	w. OR	IAE, NRCS	Miller et al. (2011)
Indian ricegrass (*Acnatherum hymenoides*)	NV, UT, AZ, WY, NM	ARS	Johnson et al. (2012)
California brome (*Bromus carinatus* Hook and Arn,)	e. OR, w. OR, n. CA	R6	Completed Internal report
Big Deer Vetch (*Lotus crassifolius*)	OR	R6	Completed Internal report
Bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve)	OR, WA, ID, NV, CA	PNWRS, ARS, RMRS	St. Clair et al. (2013)
Taper-tip onion (*Allium acuminatum*)	OR, ID, NV	ARS	Johnson et al. (2013)
Antelope bitterbrush (*Purshia tridentata* (Pursh) DC.)	e. OR, WA	PNWRS	Data collection complete
Blackbrush (*Coleogyne ramosissima*)	CA, NV, UT, n. AZ	RMRS	Data collection complete
Sulphur-flower buckwheat (*Eriogonum umbellatum*)	s. ID, se. OR	RMRS	Data collection complete
Fernleaf biscuitroot (*Lomatium dissectum* (Nutt.) Mathias and Constance)	s. ID, se. OR	PNWRS, RMRS	Data collection complete
Sanderg's bluegrass (*Poa secunda* J. Presl)	OR, WA, ID, NV, CA	PNWRS, ARS, RMRS	Data collection complete
Prairie Junegrass (*Koeleria macrantha* (Ledeb.) Schult.)	OR, WA, ID, NV, CA	PNWRS, PNW, NRCS	Data collection complete
Big sagebrush (*Artemisia tridentata*)	rangewide	RMRS	Data collection in progress
Bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey)	OR, WA	PNWRS	Data collection complete

Notes: States are OR, Oregon; CA, California; WA, Washington; NV, Nevada; UT, Utah; AZ, Arizona; WY, Wyoming; NM, New Mexico; and ID, Idaho. Parts of states are described as e., east; w., west; n., north; s., south; se., southeast. Principles are R6, USFS Pacific Northwest Region; PNWRS, USFS Pacific Northwest Research Station; ARS, USDA Agricultural Research Service; NRCS, USDA Natural Resources Conservation Service; IAE, Institute for Applied Ecology; RMRS, USFS Rocky Mountain Research Station.

† The current common garden test status is described in these sources.

climatic environments; other species are climatic generalists that show less differentiation and can be moved across a wide range of environmental gradients without a decline in fitness (Rehfeldt 1994, Johnson et al. 2010*a*). Similar information for other native taxa has lagged considerably in comparison to forest tree species. More recent studies by government agencies along with collaborators, however, have used a genecological approach such as those used for forest trees for seed zone delineation (Table 1). These studies show a similar range of climatic specialization (generalist vs. specialist), but many key species remain unstudied.

Despite the scarcity of data on adaptive genetic variation for the majority of native plant species used in restoration projects, there is demand for guidance on the choice of appropriate plant materials and how far these materials can be moved from their native environment. The most basic guidelines for seed movement involve the use of seed zones. These are geographically delineated areas within which seed can be transferred with little risk of maladaptation. The use of seed zones helps ensure that plant materials are adapted to the local environment, a key to successful restoration and revegetation (Johnson et al. 2004). Their use can also help maintain the integrity of natural genetic structure and diversity so that populations have the capacity to respond and adapt to changing biotic and abiotic environments. It is well known that ecotypic variation exists in native plants and there is a large body of literature on local adaptation and natural selection in plant populations (e.g., Linhart and Grant 1996, Leimu and Fischer 2008, Hereford 2009). However, few seed zones have been delineated for shrubs, grasses, and forbs in the United States (see Table 1) and there is a need for guidelines on seed movement that (1) can be applied across species, (2) reflect potential local adaptation to minimize maladaptation, and (3) are operationally manageable.

The objective of this project was to use high-resolution temperature and precipitation data to delineate provisional seed zones that, in combination with established ecoregions, can be used to guide movement of plant materials for restoration. These provisional seed zones are intended for use with species for which there is no specific knowledge or data available on local adaptation and population differentiation.

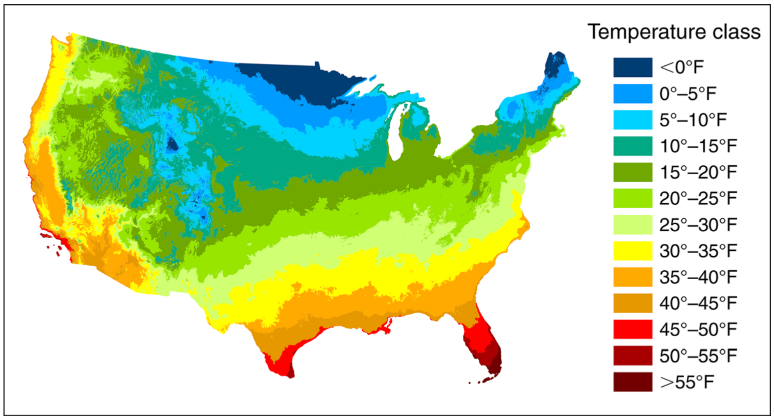

Fig. 1. Winter minimum temperature class bands. The 5°F bands correspond to 2.8°C.

Materials and Methods

Winter minimum temperature has been found to be an important factor affecting local adaptation in many species of conifers that have been studied using common garden methodology (Johnson et al. 2004). Recent studies of other native grasses, forbs, and shrubs have also shown the importance of temperature as well as precipitation (Erickson et al. 2004, Horning et al. 2008, Johnson et al. 2010*b*, 2012, 2013, St. Clair et al. 2013). However, these studies have often focused on discrete geographic areas such as the Blue Mountains of eastern Oregon or the Great Basin (parts of Nevada, western Utah, southeastern Oregon, and southern Idaho). While precipitation and temperature vary greatly within these areas, the seasonality of precipitation is relatively consistent. Across the entire continental United States, however, the timing of precipitation can vary dramatically. To account for these differences in temperature and seasonality of precipitation, we used an annual heat : moisture index as a measure of overall aridity. This allowed us to distinguish areas that are warm and wet (low–moderate aridity), cold and wet (low aridity), warm and dry (high aridity), and cold and dry (moderate–high aridity).

Climate data were obtained from the PRISM Group at Oregon State University and included raster files for mean monthly minimum and maximum temperature and annual precipitation based on climate normals for the period 1981–2010 with an 800 × 800 m cell size (data *available online*).[5] Data were imported into ArcMap version 10 (ESRI, Redlands, California, USA) for all analyses.

Minimum winter temperature was determined as the minimum value per cell from December through February and was classified into 5°F (2.8°C) bands that ranged from <10° to >55°F (–12.2° to 12.8°C; Fig. 1). These intervals were chosen to reflect the temperature bands used in the USDA plant hardiness zone map (USDA Agricultural Resource Service 2012), which is familiar to land managers and has been widely used by gardeners for decades. Annual heat : moisture index (AH:M) was used as a measure of aridity, and was calculated as mean annual temperature (MAT) plus 15°C (to obtain positive values) divided by mean annual precipitation in meters (Hamann and Wang 2005). AH:M was then divided into six discrete classes (<2, 2–3, 3–6, 6–12, 12–30, and >30), where higher values indicate more arid environments (Fig. 2). These aridity bands were slightly modified to whole integers from a geometric interval determined by ArcMap for six classes. These intervals ensure that each class range has approximately the same number of values and that the change between intervals is fairly constant (ESRI, Redlands, California, USA). The Union function of ArcMap was used to intersect the minimum winter temperature with the AH:M layer to create unique climatically delineated (temperature–aridity) zones. Polygons in the resulting layer that were less than 2.0 km^2 were eliminated to simplify delineation. Climatic zones that were represented by only a single polygon of less than 8 km^2 were merged with the adjacent zone, again to simplify delineation.

Temperature and aridity are relatively homogeneous over large geographic areas, especially in the eastern United States (Figs. 1 and 2); however, areas that may be climatically similar (within a single temperature–aridity zone) may be different ecologically (e.g., vegetation, geology, topography, soils) indicating environmental variation that should be taken into account in order to minimize maladaptation when determining seed transfer. To account for these potential ecological differences, Omernik's (1987) level III ecoregions were overlaid on the climatic zones to identify areas that differ ecologically although they may be similar climatically (GIS shapefiles *available online*).[6]

To test our model, comparisons were made among seed zones based on climate zones alone (hereafter, "provisional seed zones"), seed zones based on level III ecoregions alone, seed zones based on provisional seed

[5] http://www.prismclimate.org

[6] http://www.epa.gov/naaujydh/pages/ecoregions/level_iii.htm

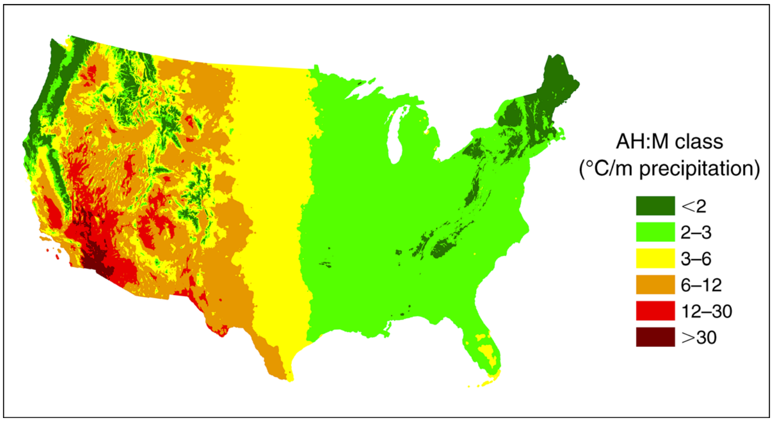

FIG. 2. Annual heat : moisture (AH:M) index class bands. AH:M was calculated as mean annual temperature (MAT, °C) plus 15°C (to obtain positive values) divided by mean annual precipitation in meters (Hamann and Wang 2005).

Communications

zones nested within level III ecoregions, and empirical seed zones derived from common garden studies of individual species. Empirical seed zones are derived based on overlapping multiple traits (St. Clair et al. 2013), and results for any single trait may differ among classification schemes; taken together, however, empirical zones may be considered best for the suite of traits thought to be most important for adaptation as determined in individual studies. We tested a suite of traits that could be important in local adaptation, but this analysis was not intended to determine which traits are or are not important for local adaptation. We determined how much of the variation in traits among populations was accounted for by the different classification schemes. Ideally, a greater proportion of the total population variation should exist among seed zones and less variation should exist within seed zones for the suite of traits potentially important for adaptation. However, it is difficult to know which traits are most important for adaptation for each species in the wild, making it challenging to directly compare the performance of different seed zone classification systems. We tested a suite of traits that might logically be associated with fitness; data for traits of phenology, morphology, and growth from three common garden studies (Johnson et al. 2012, 2013, St. Clair et al. 2013) for two grasses and one forb were used to compare seed zone classifications. Components of variance for locations (i.e., populations) were obtained from SAS PROC MIXED (SAS Version 9.3 for Windows; SAS Institute, Cary, North Carolina, USA) both with and without different classification schemes in the model. The percentage of variance explained by the classification scheme was calculated as $(([\sigma^2_L - \sigma^2_{L(Z)}]/\sigma^2_L) \times 100$, where σ^2_L and $\sigma^2_{L(Z)}$ are the variance components for location without zones and location within zones, respectively.

RESULTS

We divided continuous climate into discrete bands resulting in the delineation of 13 winter minimum temperature bands (Fig. 1) and six AH:M bands (Fig. 2). The intersection of winter minimum temperature bands with AH:M bands resulted in 64 climatic zones across the continental United States (Fig. 3) with a total of 20 695 polygons ranging in size from 2.0 to over 480 919 km^2. Geographic variation in temperature and aridity differ dramatically between the eastern and western United States (east and west of approximately 104° W; Figs. 1 and 2), largely reflecting differences in topography, and the number and average size of the climatic zones differ accordingly (Fig. 3). The western United States (from Montana to New Mexico and west) has 10 more climatic zones than the eastern United States has (of the 64 zones total, 60 occur in the western United States and 50 in the eastern United States), however, there are almost 3.5 times more polygons in the western United States compared to the eastern United States (16 116 vs. 4655) and the average area of the zones in the western United States is only one-fifth the size of the eastern United States zones (253.9 km^2 vs. 1250.3 km^2; Fig. 3). The homogeneity across the landscape and larger size of the climatic zones in the eastern United States is clearly evident in Fig. 3.

All four methods of seed zoning were effective in partitioning the population variation among zones for most traits, although some traits showed little variation among zones (Table 2). It is difficult to compare the different studies for different species since none of the studies directly measures adaptation, but rather traits that help determine adaptation. Comparing just climatic zones (provisional seed zones) and level III ecoregions, they were nearly equally effective at partitioning population variation for the traits considered, with either classification explaining a larger percentage of the variation than the other in approximately one-half the traits (15 and 13 of 28 traits; Table 2). Overall, provisional seed zones nested within level III ecoregions were the best at explaining variation among populations: in 12 out of 28 comparisons, this method explained more variance than the other three methods and was tied with another method in 4 out of 28 comparisons. Empirical seed zones were superior in 12 out of 28 comparisons, while zones based on either level

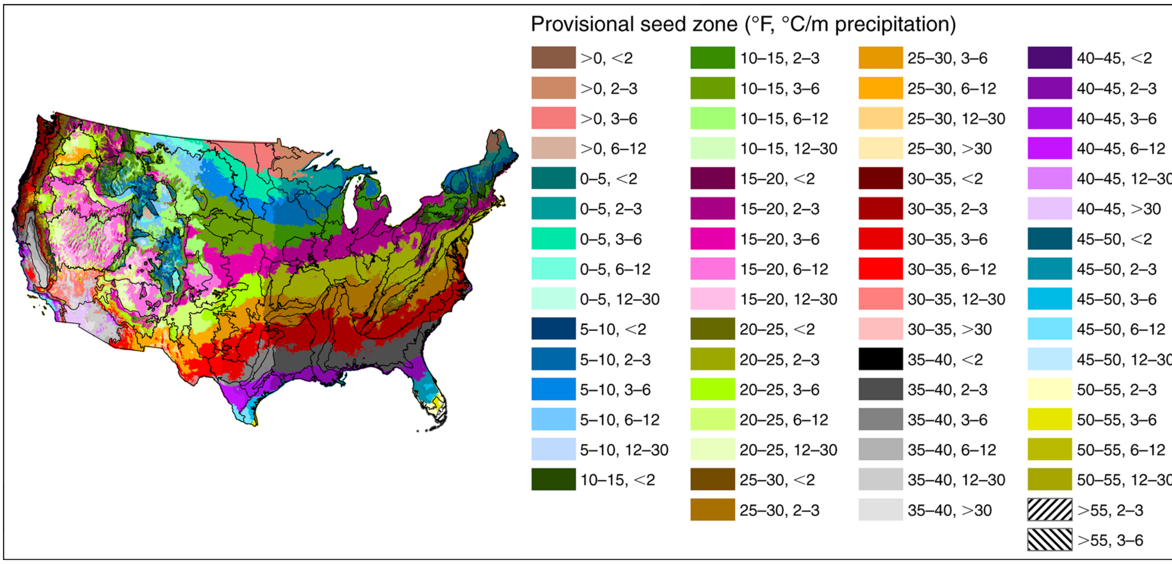

Fig. 3. Provisional seed zones for native plants (color polygons) overlain with Omernik's (Omernik 1987) level III ecoregion boundaries (black lines). We recommend using the provisional seed zones as the first step in defining seed transfer guidelines, and that level III ecoregions be used to refine seed movement within a provisional seed zone. In the legend, the first range of numbers is the temperature class band (°F) and the second range of numbers is the AH:M index class bands (°C/m precipitation). See the Appendix for a larger version of this figure.

III ecoregions or climate alone both tied for most explanatory power in only four cases.

Discussion

Seed zones are needed for species used in restoration for which we do not have information on the spatial distribution of genetic variation in adaptive traits that can be used to guide seed transfer. Gene flow tends to limit local adaptation as it acts to homogenize allele frequencies among populations (Hereford 2009). It is generally assumed that local adaptation increases with distance among populations as a result of reduced gene flow and the resulting genetic differentiation among populations (Leimu and Fischer 2008). However, ecological distance is often a better predictor of local adaptation than geographic distance, and therefore likely a better indicator of potential success in restoration (McKay et al. 2005, Noël et al. 2011). The provisional seed zones proposed here delineate areas of climatic similarity, which when combined with areas of general ecological similarity delineated by level III ecoregions, may be effective as a starting point for guiding seed transfer of species used in restoration. The use of level III ecoregions to limit seed transfer within provisional seed zones is supported by the results of the comparison of various classification schemes (Table 2). Provisional seed zones delineated by climatic zones within level III ecoregions resulted in more variation partitioned among zones than either climatic zones alone or ecoregions alone. This result is not unexpected since climatic zones within level III ecoregions resulted in a larger number of zones by a factor of five or more than either alone (Table 2). Despite the higher proportion of variation explained, the trade-off of further subdividing provisional seed zones by level III ecoregions is that it may result in too many zones to be practical from a land management perspective. To make the juxtaposition of provisional seed zones and level III ecoregions most efficient and useful for management, we recommend that provisional seed zones based on climate alone form the basis of seed zone delineation, and that level III ecoregions be used to refine seed movement within a provisional seed zone.

Because provisional seed zone boundaries are the result of discrete intervals imposed on an often continuous climatic gradient, and because ecoregion boundaries similarly can represent continuous, rather than discrete changes in vegetation, seed zone boundaries should be interpreted with caution. Although widely separated ecoregions may differ significantly climatically and/or ecologically, in many locations climatic differences among locations in adjacent ecoregions, especially near adjacent ecoregion boundaries, may not be great. Accordingly, transfers between sites within a provisional seed zone on opposite sides but close to the boundary between adjacent ecoregions may be acceptable and should be evaluated on a case-by-case basis, using local knowledge and expertise. Based on the abundant evidence for local adaptation in plant populations (Linhart and Grant 1996, Leimu and Fischer 2008; Tables 1 and 2) we feel that transfers between widely separated, nonadjacent ecoregions, or geographically distant transfers, may be undesirable and to be conservative, we feel should be avoided.

The heterogeneous terrain of the western United States results in areas with many provisional seed zones across the landscape (Fig. 3). In many regions, however, a substantial proportion of the acreage in a given area

TABLE 2. Comparison of percentage of variation explained by classification scheme for three common garden studies.

Trait	Variation accounted for (%)			
	Level III	Prov SZ	Prov SZ(III)	Emp. SZ
Allium accuminatum (Johnson et al. 2013)				
Number of zones	5	9	41	6
Flowering date	0.02	*16.26*	16.26	**37.24†**
Bolting date	4.99	*22.01*	23.96	**56.83†**
Maturity date	2.50	*8.01*	**10.86†**	7.28
Flower to bolt days	7.27	*25.81*	30.40	**57.70†**
Scape length : diameter	*5.76*	0.63	**6.24†**	2.59
Flower color	*29.84‡*	2.92	**29.84‡**	12.77
No. leaves	17.38	*34.24*	**42.74†**	24.19
No. flowers/umbel	0.00	*9.67*	9.67	**30.53†**
No. seeds/plant	0.00	*48.94‡*	**48.94‡**	24.65
Achnatherum hymenoides (Johnson et al. 2012)				
Number of zones	12	17	85	13
Heading date	*17.63*	0.96	19.09	**20.98†**
Bloom date	0.04	*15.34*	15.34	**31.32†**
Maturity date	*4.61*	0.08	4.57	**16.22†**
Bloom to maturity	0.00	*31.18*	31.18	**50.74†**
Leaf length × width	6.63	*11.32*	**34.21†**	0.00
Culm length	*10.63*	7.97	**17.71†**	4.24
Panicle length	2.94	*8.14*	9.73	**10.04†**
Plant habit	*15.22‡*	14.99	**15.22‡**	5.21
Leaf roll	9.98	*26.93*	**31.60†**	27.07
Dry mass	5.47	*9.10*	**14.32†**	0.04
No. seeds/panicle	*23.04*	5.53	23.11	**23.86†**
Pseudoroegneria spicata (St. Clair et al. 2013)				
Number of zones	12	13	87	11
Heading date	*14.57*	9.98	16.92	**19.27†**
Bloom date	*30.06*	8.78	**32.86†**	12.37
Maturity	0.06	*9.26‡*	**9.26‡**	0.00
Leaf pubescence	*22.72*	10.85	**25.43†**	22.32
Leaf length : width	18.02	*33.94*	**38.50†**	34.98
Plant height	*5.09*	4.44	12.37	**18.61†**
Dry mass	*31.71*	27.45	**48.53†**	37.67
No. flowers	*37.71*	21.74	**51.45†**	31.71

Notes: The common garden studies are Level III, Omernik's level III ecoregion; Prov SZ, provisional seed zone based on climate information only; Prov SZ(III), provisional seed zone nested within level III ecoregion; and Emp. SZ, species-specific empirically determined seed zone. Values in italic type are the larger of level III and provisional zone values, values in boldface type are the larger of provisional seed zone within level III ecoregion and empirical seed zone values.

† Indicates which seed zone delineation method explained the most variation for each trait.

‡ Indicates where two seed zone delineation methods performed equally.

usually falls into a limited number of seed zones. For example, there are 21 provisional seed zones in the Pacific Northwest (Oregon and Washington) (covering 425 000 km^2), but 87% of the area (369 720 km^2) is contained in just 8 zones, and 98% of the area in 13 zones. Similarly, in the Great Basin, there are 17 provisional seed zones (covering 505 785 km^2) with 90% of the area (458 600 km^2) contained in just 5 zones and 98% in 8 zones. In addition, a given species is only likely to be found in areas of certain climatic conditions, and therefore, in only a subset of the seed zones, and restoration is unlikely to be needed in some of these seed zones due to infrequent disturbances or management activity (e.g., high-elevation areas). Seed collection and production for specific seed zones can be tailored to the zones most appropriate for a given species depending on its temperature and aridity tolerances.

Empirically derived seed zones and seed transfer guidelines should ideally be based on species-specific data collected from short- and long-term tests; however, information on genetic differentiation and adaptation from such tests are lacking for many native plants. A number of common garden studies of important restoration species in the western United States are planned, under way, or complete, and results have been published for several species (Table 1). These empirically designed seed zones should supersede the provisional seed zones, since, by design, the provisional seed zones are intended for species for which we have no specific data on genetic variation. Additionally, these provisional seed zones can be adapted to accommodate future climate change simply by replacing the PRISM climate normal data with predicted future temperature and aridity data (based on a chosen climate model, emission scenario, and timeframe), and repeating the intersection of the updated shapefiles.

To allow end-users to view and acquire data on seed zones for use in plant material development, gene conservation and native plant restoration activities, these provisional seed zones, along with empirical seed zones for some native plants, are available in the Seed Zone Mapper application, part of a family of Wildland Threat Mapping (WTM) applications developed by the Western Wildlands Environmental Threat Assessment Center (WWETAC) to portray the spatial interactions of wildland threats and high value resources that occur in wildlands (*available online*).[7]

Acknowledgments

The authors acknowledge R. C. Johnson for supplying common garden data, Ken Vance-Borland who provided assistance with GIS analysis, and Charlie Schrader-Patton who was instrumental in developing the Seed Zone Mapper application on the WWETAC website, and the anonymous reviewers whose comments have improved the manuscript.

Literature Cited

Aitken, S. N., S. Yeaman, J. A. Holliday, T. Wang, and S. Curtis-McLane. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary Applications 1:95–111.

Chimura, D. J., P. D. Anderson, G. T. Howe, C. A. Harrington, J. A. Halofsky, D. L. Peterson, D. C. Shaw, and J. B. St. Clair. 2011. Forest responses to climate change in the northwestern United States: ecophysiological foundations for adaptive management. Forest Ecology and Management 261:1121–1142.

Doede, D. L. 2005. Genetic variation in broadleaf lupine (*Lupinus latifolius*) on the Mt. Hood National Forest and implications for seed collection and deployment. Native Plants Journal 6:36–48.

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., N. L. Mandel, and F. C. Sorensen. 2004. Landscape patterns of phenotypic variation and population structuring in a selfing grass, *Elymus glaucus* (blue wildrye). Canadian Journal of Botany 82:1776–1789.

Hamann, A., and T. Wang. 2005. Models of climatic normal for genecology and climate change studies in British Columbia. Agricultural and Forest Meteorology 128:211–221.

Hereford, J. 2009. A quantitative survey of local adaptation and fitness trade-offs. American Naturalist 173(5):579–588.

Horning, M. E., T. R. McGovern, D. C. Darris, N. L. Mandel, and R. Johnson. 2008. Genecology of *Holodiscus discolor* (Rosaceae) in the Pacific Northwest, U.S.A. Restoration Ecology 2008:1–9.

Johnson, G. R., F. C. Sorensen, J. B. St. Clair, and R. C. Cronn. 2004. Pacific Northwest forest tree seed zones: a template for native plants? Native Plants Journal 5:131–140.

Johnson, G. R., L. Stritch, P. Olwell, S. Lambert, M. E. Horning, and R. Cronn. 2010*a*. What are the best seed sources for ecosystem restoration on BLM and USFS lands? Native Plants Journal 11:117–131.

Johnson, R. C., M. J. Cashman, and K. W. Vance-Borland. 2012. Genecology and seed zones for Indian ricegrass collected in the southwestern United States. Rangeland Ecology and Management 65:523–532.

Johnson, R. C., V. J. Erickson, N. L. Mandel, J. B. St. Clair, and K. W. Vance-Borland. 2010*b*. Mapping genetic variation and seed zones for *Bromus carinatus* in the Blue Mountains of eastern Oregon, USA. Botany 88:725–736.

Johnson, R. C., B. C. Hellier, and K. W. Vance-Borland. 2013. Genecology and seed zones for tapertip onion in the US Great Basin. Botany 91:686–694.

Leimu, R., and M. Fischer. 2008. A meta-analysis of local adaptation in plants. PLoS ONE 3(12):e4010.

Linhart, Y. B., and M. C. Grant. 1996. Evolutionary significance of local genetic differentiation in plants. Annual Review of Ecology and Systematics 37:237–277.

McKay, J. K., C. E. Christian, S. Harrison, and K. J. Rice. 2005. "How local is local"—A review of practical and conceptual issues in the genetics of restoration. Restoration Ecology 13(3):432–440.

Miller, S. A., A. Bartow, M. Gisler, K. Ward, A. S. Young, and T. N. Kaye. 2011. Can an ecoregion serve as a seed transfer zone? Evidence from a common garden study with five native species. Restoration Ecology 19:268–276.

Noël, F., D. Prati, M. van Kleunen, A. Gygax, D. Moser, and M. Fischer. 2011. Establishment success of 25 rare wetland species introduced into restored habitats is best predicted by ecological distance to source habitats. Biological Conservation 144:602–609.

Omernik, J. M. 1987. Ecoregions of the conterminous United States. Annals of the Association of American Geographers 77:118–125.

Rehfeldt, G. E. 1994. Evolutionary genetics, the biological species, and the ecology of the Interior cedar-hemlock forests. Pages 93–100 *in* Proceedings of the interior cedar–hemlock–white pine forests: ecology and management. 1993 March 2–4; Spokane, WA. Department of Natural Resource Sciences, Washington State University, Pullman, Washington, USA.

St. Clair, J. B., F. F. Kilkenny, R. C. Johnson, N. L. Shaw, and G. Weaver. 2013. Genetic variation in adaptive traits and seed transfer zones for *Pseudoroegneria spicata* (bluebunch wheatgrass) in the northwestern United States. Evolutionary Applications 6:933–938.

USDA Agricultural Resource Service. 2012. Plant hardiness zone map. http://planthardiness.ars.usda.gov/PHZMWeb/

USDA Forest Service. 2012*a*. Increasing the pace of restoration and job creation on our National Forests. U.S. Forest Service, Washington, D.C., USA.

USDA Forest Service. 2012*b*. Native Plant Materials Policy; a strategic framework. Report FS-1006. U.S. Forest Service, Washington, D.C., USA.

Wilson, B. L., D. C. Darris, R. Feigner, R. Johnson, M. E. Horning, and K. Kuykendall. 2008. Seed transfer zones of a native grass *Festuca roemeri* genecological evidence. Native Plants Journal 9:287–302.

Supplemental Material

Appendix

Provisional seed zones for native plants (color polygons) overlain with Omernik's (Omernik 1987) level III ecoregion boundaries (black lines). We recommend using the provisional seed zones as the first step in defining seed transfer guidelines, and that level III ecoregions be used to refine seed movement within a provisional seed zone (*Ecological Archives* A024-053-A1).

[7] http://www.fs.fed.us/wwetac/threat_map/SeedZones_Intro.html