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Genecology and seed zones for tapertip onion in the US Great Basin

R.C. Johnson, Barbara C. Hellier, and Ken W. Vance-Borland

Abstract: The choice of germplasm is critical for sustainable restoration, yet seed transfer guidelines are lacking for all but a few herbaceous species. Seed transfer zones based on genetic variability and climate were developed using tapertip onion (*Allium acuminatum* Hook.) collected in the Great Basin and surrounding areas in the United States. Bulbs from 53 locations were established at two common garden sites and morphological (such as leaf and scape dimensions), phenological (such as bolting date and flowering), and production traits (such as emergence and seeds per plant) were measured. Differences among source locations for plant traits within both common gardens were strong ($P < 0.001$), indicating genetic variation. Principal component 1 (PC 1) for phenological traits, with $R^2 = 0.59$, and PC 1 for production traits, with $R^2 = 0.65$, were consistently correlated with annual, maximum, minimum, and average temperature, annual precipitation, and frost-free days at source locations ($P < 0.05$). Regression of PC 1 phenology and PC 1 production scores with source location climates resulted in models with R^2 values of 0.73 and 0.52, respectively. Using a geographic information system, maps of these models were overlaid to develop proposed seed zones to guide the choice of germplasm for conservation and restoration of tapertip onion across the collection region.

Key words: Allium acuminatum, genecology, genetic resources, restoration.

Résumé : Le choix des germoplasmes revêt une importance critique pour la restauration durable : pourtant, les lignes directrices pour le transfert des semences font défaut, à quelques exceptions près, pour l'ensemble des espèces herbacées. Les auteurs ont développé des zones de transfert des semences basées sur la variabilité génétique et le climat, en utilisant l'oignon acuminé (*Allium acuminatum* Hook.) récolté à Grand Basin et ses environs, aux États-Unis. Ils ont planté des bulbes provenant de 53 localités sur le site de deux jardins communs et ils ont mesuré les traits morphologiques (tels que les dimensions des feuilles et des hampes), phénologiques (tels que la date de floraison et la montée à graines) et les caractères de production (tels que l'émergence et le nombre de graines par plant). Les différences entre les localités d'origine pour les traits des plantes à l'intérieur des deux jardins communs sont robustes ($P < 0,001$), traduisant la variation génétique. L'analyse en composantes principales 1 (PC 1) pour les traits phénologiques, avec $R^2 = 0,59$, et PC 1 pour les traits de production, avec $R^2 = 0,65$, montre une corrélation congrue avec les températures, annuelles, maximales, minimales et moyennes, la précipitation annuelle ainsi que le nombre de jours sans gel sur la localité des sources ($P < 0,05$). La régression du PC 1 sur la phénologie et le PC 1 des données de production, avec les climats des localités d'origine, conduit à des modèles ayant des valeurs de 0,73 et 0,52, respectivement. En utilisant le système d'information géographique, on a superposé la carte de ces modèles afin de proposer des zones de semences pour guider le choix des germoplasmes en vue de la restauration et la conservation de l'oignon acuminé, sur l'ensemble de l'aire des récoltes. [Traduit par la Rédaction]

Mots-clés : Allium acuminatum, génécologie, ressources génétiques, restauration.

Introduction

Restoration using native species is increasingly critical for improving habitat quality in arid and semiarid landscapes. Large areas of the arid western USA have been severely degraded by uncharacteristically frequent wildfires (Hessburg et al. 2005), overgrazing (Knapp 1996), and invasive weeds, especially *Bromus tectorum* L. (Knapp 1996). As climate change interacts with these factors, pressure on plant communities will continue (Kramer and Havens, 2009; Westerling et al. 2006), threatening both plant and animal habitat (Schroeder et al. 2004).

With the ongoing need for restoration, there is a need to define seed zones, delineated areas to guide seed transfer, so germplasm used for restoration is well suited and, to maximize efficient use of resources, originates from as wide a geographic area as possible. Although reciprocal transplant studies can directly evaluate local adaptation (Rice and Knapp 2008), 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 (Kawecki and Ebert 2004). Common garden experiments are a way

to quantify genetically based phenotypic differences among a relatively large number of plant populations (Campbell 1986; Rehfeldt 1994; St Clair et al. 2005; Johnson et al. 2010, 2012) and to assess environmental factors as a selection force driving local adaptation (Kawecki and Ebert 2004; Miller et al. 2011; Weißhuhn et al. 2012). For genecology studies, genetic traits from common gardens are related to plant source climates using regression modeling and geographic information system (GIS) mapping (St Clair et al. 2005; Johnson et al. 2010, 2012).

Genecology has principally focused on commercially important conifer tree species (Campbell 1986; Rehfeldt 1994; St Clair et al. 2005). There have been genecology studies on certain grasses (Erickson et al. 2004; Wilson et al. 2008; Johnson et al. 2010, 2012), ocean spray (*Holodiscus discolor* (Pursh) Maxim.) (Horning et al. 2010), and on a relatively small region for broadleaf lupine (*Lupinus latifolius* Lindl. ex J. Agardh) (Doede 2005). But in general, research concerning the diversity and the appropriate scale of plant movement for most native shrub, grass, and especially forb species is very limited (Hufford and Mazer 2003; McKay et al. 2005; Walker and Shaw 2005).

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Forbs in general, which include wild onion (*Allium* spp.), are an important component of sage grouse (*Centrocercus urophasianus* Bonaparte, 1827) diet, especially for juvenile sage grouse before brood dispersal (Drut et al. 1994; Nelle et al. 2000). Tapertip onion (*Allium acuminatum* Hook.) is a common forb species native to the Western U.S. and British Columbia (http://plants.usda.gov/java/ profile?symbol=ALAC4). It is often found on rocky or gravelly sites in the sagebrush–steppe community typical of the Great Basin and surrounding areas. It reproduces by seeds and also clonally by the splitting or daughtering of subterranean bulbs. Relatively high outcrossing rates are likely, given its protandry, along with the active, polylectic foraging by native bees, especially *Osmia* sp. (Hatley 1981). Its early flowering may support foraging native bees before other, later species flower. In this study, tapertip onion collected from the Great Basin and surrounding areas was used in common garden research to (*i*) determine if and to what extent variation in morphological, phenological, and production traits across the Great Basin was linked to source location climatic variables; (*ii*) visualize genetic variation as a function of source location climate through regression modeling and GIS mapping; and (*iii*) develop seed transfer zones to promote sustainable restoration for tapertip onion in the Great Basin.

Material and methods

Plant collection and establishment

Populations of bulbs were collected from diverse geographic and climatic areas in mid-June to early July of 2005 from native populations across southern Oregon and Idaho and northeastern Nevada (Adair et al. 2006). Germplasm was collected as bulbs because mature umbels are difficult to spot and fragile scapes are often broken, dispersing seeds soon after maturity. Bulbs were sampled from more than 30 plants over an area greater than 2500 m². They were globe shaped, so diameter was used as an index of size (Adair et al. 2006). Bulbs from 55 populations were stored in a dormant state at 14 °C, 40%–50% relative humidity until planted in a greenhouse in September 2005. The soil media was Sunshine #4 potting soil (Sun Gro Horticulture, Vancouver, British Columbia, Canada) amended, by volume, to contain 50% perlite. After diameter measurements, bulbs were placed 5 cm deep into individual cells 12.7 cm tall with a 2.6 cm wide opening within "books" of four cells (Spencer-Lemaire Industries, Edmonton, Alberta, Canada). Sown bulbs were maintained in the greenhouse for one month in the fall of 2005 and then placed in a vernalization chamber at 4 °C. Bulbs from most source locations sprouted during the vernalization treatment. Plants were removed from vernalization after four months and transplanted to common gardens in March 2006 at Central Ferry (CF), Washington (46°40′9″N, −117°45′21″W), and in April 2006 at Pullman (PU), Washington (46°43′9″N, −117°8′9″W).

After the post-transplant period in 2006, the bulbs became dormant in the fall. During the experimental year between 1 September 2006 and 30 August 2007, precipitation at CF and PU was 383 and 433 mm, respectively. Average precipitation at source locations ranged from 252 to 792 mm. During the same period, average monthly minimum and maximum temperatures ranged from −0.51 °C to 25.3 °C at CF, and from −3.43 °C to 20.6 °C at PU. For source locations, those monthly averages ranged from −3.46 °C to 18.7 °C.

Experimental design and plant culture

Plants were randomized in complete blocks with five replications. Each replication was a subsample of four bulbs from a given source location, resulting in 20 plants for each of the 55 source locations at each common garden site. Within each plot, the four bulbs were spaced 7 cm apart in a square pattern. Plots were spaced 0.6 m apart in rows, and rows were spaced 2 m apart. No irrigation or fertilizer was applied. Many plants senesced soon after being transplanted in 2006, so data collection on plants from the majority of source locations was not possible that year. In 2007, plants emerged from all but two of the 55 locations. Data were collected for the phenological, morphological, and production measurements, as described in Table 1.

Statistical analysis

ANOVA was completed on each plant trait in Table 1 using the mixed procedure (PROC MIXED) in SAS/STAT version 9.2, as described in Littell et al. (1996), with bulb diameter as a covariate for evaluating maternal effects. Blocks within source locations were assumed to be random, and garden sites, locations, and bulb diameter fixed effects. For principal component analysis (PCA), only variables with significant ($P < 0.01$) source location effects or source location × garden site effects were considered. Given the large number of traits analyzed and the high error df, the $P < 0.01$ level was used to ensure a strong probability of detecting only true differences for locations and interactions.

If the location × site was not significant, then the data from sites were averaged; if the location × site was significant ($P < 0.01$), the site data were averaged if correlation between sites exceeded $r = 0.80$. We reasoned that if a large fraction of the variation was explained by the correlation between sites, the inclusion of data from both sites would be redundant. The traits were organized into morphological, phenological, and production categories, with PCA conducted on each group of traits using SAS PRINCOMP. This included the Eigenvalues for determining R^2 values, the loading coefficients for each PCA equation, and the PCA scores.

Elevation, latitude, and longitude were obtained from geographic positioning instrumentation in situ for each wildland source location. Climate data at source locations were 30-year averages derived from the Climate Western North America web site (http://www. genetics.forestry.ubc.ca/cfcg/ClimateWNA/ClimateWNA.html) using PRISM spatial models (Daly et al. 2008; http://www.ocs.orst.edu/ prism) at a resolution of 30 arcsec (≈800 m grids). Climatic variables included monthly and annual minimum, maximum, and average temperatures at each collection source location; monthly and annual precipitation; and date for 50% probability of the last spring frost, first autumn frost, and the frost-free period. The Pearson linear correlation coefficient (r) was used to relate plant traits to geographic and climatic variables.

Regression modeling was completed on bolting, seeds per plant, and PCA scores as composite plant traits. Each plant trait as the dependent variable was regressed on climatic variables, longitude and latitude, and elevation, the independent variables, at source locations using SAS PROC REG. The objective was to find models with the highest predictive value with the fewest number of model parameters (Draper and Smith 1998). Within PROC REG, the maximum R^2 improvement (MAXR) option was used, along with the Mallows's C_p statistic (Mallows 1973) to minimize over parameterization. For a given plant trait, all environmental variables from source locations were included and the maximum R^2 and C_p statistic calculated progressively, starting with the one environmental variable producing the highest R^2, then two, and so forth, for all environmental variables. The model selected was the maximum R^2 model when additional variables caused the C_p statistic to increase, the point when adding variables only marginally improved the R^2. These were best-fit models to maximize predictions so coefficients and variables are designed to function as a set; owing to correlations among variables in the regression, they do not necessarily identify the most important single, independent geographic or climate variables for a given trait.

Mapping and seed zone development

Spatial mapping of bolting, seeds per plant, and principal component 1 (PC 1) scores for the phenology and production groups predicted from regression models was completed using the grid algebra function (raster calculator) of the ArcGIS 9.3

Table 1. Measured and derived plant traits for tapertip onion taken in the spring and summer of 2007 in common gardens at Central Ferry and Pullman, Washington, USA.

Trait	Measurement description
Morphology	
Leaf length (mm)	Measured at bolting
Leaf width (mm)	Measured at mid-leaf at bolting
Leaf length to leaf width ratio	Derived
Scape length (mm)	Length of scape from the soil to umbel base
Scape diameter (mm)	Measured at mid-scape
Scape length to scape diameter ratio	Derived
Umbel diameter (mm)	Measured when 50% of the flowers were in bloom
Flower color	Rated from 1 (white) to 9 (purple)
Phenology	
Bolting date	Day of year when the scape exceeded 20 mm
Flowering date	Day of year when 50% of the flowers were open
Days to seed maturity	Day of year when 50% of seed capsules were open
Days bolting to flowering	Derived
Days flowering to seed maturity	Derived
Days bolting to maturity	Derived
Production	
Emergence	Emergence from bulbs in 2007 after the 2006 planting
Leaf number	Number of leaves per plant
Flowers per umbel	Flowers per umbel per plant
Seeds per plant	Harvested seeds per plant

Table 2. Summary of analyses of variance of plant traits from 53 tapertip onion collections measured in common garden sites at Central Ferry and Pullman, Washington, USA, and with initial bulb diameter as the covariate.

Trait	Mean	Site		Source location		Site × location		Covariate: bulb diameter	
		F value	P value	F value	P value	F value	P value	F value	P value
Morphology									
Leaf length (mm)	127	0.22	0.654	4.11	<0.001	1.19	0.188	0.72	0.397
Leaf width (mm)	2.65	24.7	0.001	3.31	<0.001	0.77	0.880	4.14	0.043
Leaf length to leaf width	49.6	11.7	0.009	2.1	<0.001	0.93	0.614	0.66	0.419
Scape length (mm)	150	0.75	0.413	4.74	<0.001	0.94	0.600	1.71	0.192
Scape diameter (mm)	2.58	20.6	0.002	2.41	<0.001	0.82	0.813	1.15	0.285
Scape length to diameter	60.7	16.0	0.004	2.9	<0.001	0.92	0.630	0.57	0.449
Umbel diameter (mm)	52.2	2.29	0.169	3.22	<0.001	1.09	0.318	3.11	0.079
Flower color	7.07	15.5	0.004	39.2	<0.001	2.47	<0.001	0.04	0.845
Phenology									
Bolting date	108	1152	<0.001	11.59	<0.001	1.25	0.127	0.5	0.479
Flowering date	147	920	<0.001	5.3	<0.001	1.1	0.309	0.15	0.697
Days to seed maturity	175	7033	<0.001	4.63	<0.001	1.37	0.055	1.1	0.294
Days bolting to flowering	39	95.3	<0.001	5.87	<0.001	1.67	0.004	0.07	0.798
Days flowering to seed maturity	28	202	<0.001	2.45	<0.001	1.51	0.017	2.34	0.127
Days bolting to maturity	57	71.9	<0.001	1.89	<0.001	1.32	0.077	0.1	0.750
Production									
Emergence frequency	0.60	16.5	0.004	3.94	<0.001	1.46	0.026	0.18	0.673
Leaf number	2.56	0.38	0.556	2.46	<0.001	1.13	0.255	0.21	0.646
Flowers per umbel	28.3	7.03	0.029	2.54	<0.001	0.58	0.991	1.78	0.182
Seeds per plant	65.6	46.1	<0.001	3.27	<0.001	1	0.487	1.63	0.202

Spatial Analyst extension (ESRI, Redlands, Calif., USA). Each environmental variable was multiplied by its respective regression coefficient and the results summed. Map boundaries were limited to the Omernik level III ecoregions (Omernik 1987) where plant material was collected. This included the Blue Mountains, the Idaho Batholith, the Snake River Plain, the Northern Basin and Range, and the Central Basin and Range. Mapped areas were also confined to the range of observed values for the 53 source locations. For mapping the PC traits, this was the range between the observed maximum and minimum PC scores. A mapping contour interval corresponding to the 95% confidence level at regression model means was calculated based on the regression error term derived from regression models.

Seed zones delineating areas of similar plant trait variation were created by classifying rasters for phenology PC 1 and for production PC 1 into high, medium, and low categories over the range of the data, and then overlaying the resulting rasters, similar to St Clair et al. (2005). The spatial combination (overlays) of PCs for the three classifications resulted in nine seed zones combining attributes of both phenology and production.

Results

Analyses of variance and principal components

Garden sites differed for 13 of the 18 evaluated traits ($P < 0.01$) and were particularly strong for phenology-related traits (Table 2).

Compared with CF, the cooler, wetter PU site had later phenology, along with higher bulb emergence and seed production, revealing a general plasticity response (Scheiner and Goodnight 1984) between sites.

For source locations, all 18 traits analyzed were significant at $P < 0.001$, indicating genetic variation among source locations within gardens. In most cases, the site × location interaction was not significant ($P < 0.01$) and above $P = 0.10$ for 12 of the 18 traits (Table 2). As a result, most trait means were averaged over garden sites to simplify the PCA. Several interactions had P values between 0.01 and 0.05, especially for phenology traits, so some detail regarding the site difference may have been lost in the averaging process. Still, the $P < 0.01$ working P level ensured that traits used for PCA and regression modeling strongly indicated genetic variation across locations.

Even though flower color had a significant location × site interaction, the correlation between sites was strong, explaining almost two-thirds of the variation ($r = 0.80$, $P < 0.0001$, $n = 219$). Thus, sites for flower color were considered redundant, and the CF site, having the higher F ratio, was used for further analyses. The correlation between sites for days from bolting to flowering, however, explained only 4% of the variation ($r = 0.20$, $P < 0.002$, $n = 219$), so days from bolting to flowering at each site were considered as separate plant traits for further analysis.

Because bulbs collected in situ were used to plant the common gardens, differences in bulb size associated with source locations (Adair et al. 2006) could affect growth and development through material effects (Roach and Wulff 1987; Galloway and Etterson 2007; Herman and Sultan 2011). As a covariate, however, bulb size had little or no effect on garden traits (Table 2). Only leaf width and umbel diameter had P values less than 0.10; most were much higher. Thus, there was no evidence of maternal effects and garden traits were used without further correction for bulb size.

For morphology, the first PCA represented 46% of the variation (Table 3). For phenology and production traits, the first PCA was stronger, explaining more than 59% of the variation. Thus PC 1, especially for phenology and production, represented simplified, composite plants traits useful for regression modeling and seed zone mapping.

Correlation between plant traits and environment

For certain morphological traits, there were correlations between latitude and elevation but no significant correlation between temperature variables, and only one correlation between annual precipitation and morphological traits at $P < 0.05$ (Table 4). Correlation of environmental variables and PC 1 and PC 2 morphology followed the same general pattern as seen with individual plant traits (Table 4).

Correlations between phenological and production traits and precipitation and temperature variables were frequent (Table 4). For phenology, days to bolting and days from bolting to flowering were the traits most frequently correlated with precipitation and temperature factors. For production traits, emergence and seeds per plant were correlated with annual precipitation and all temperature variables (Table 4). The composite PC 1 phenology and PC 1 production traits generally correlated with climatic variables and elevation.

Overall, plants from cooler source locations with shorter frost-free periods appeared genetically predisposed to bolt later than those from warmer locations. Yet development from bolting to flowering tended to be more rapid at cooler source locations. Plants from cooler, higher precipitation locations also produced more seeds per plant in common gardens than those from warmer, drier locations.

Because there were strong links observed among climatic variables, phenology, and production, but weak or absent links between morphology and climate, the regression modeling and mapping of traits with climate variables was confined to phe-

Table 3. Eigenvalues, percent variation explained, and total variation for principal components based on morphological, phenological, and production traits in tapertip onion collected in the Great Basin and grown in common gardens.

Principal component	Eigenvalue	R^2	% Cumulative variation explained
Morphological			
1	3.69	0.461	46.1
2	2.53	0.317	77.8
3	0.72	0.090	86.8
4	0.55	0.069	93.7
Phenological			
1	2.95	0.590	59.0
2	1.40	0.281	87.1
3	0.37	0.074	94.5
4	0.23	0.046	99.1
Production			
1	2.61	65.2	65.2
2	0.69	17.3	82.5
3	0.50	12.5	95.0
4	0.20	0.050	100

Note: Morphological traits were leaf and scape length, leaf width, scape and umbel diameter, leaf length to width, scape length to diameter averaged over sites, and flower color at the Central Ferry (CF) site in Washington, USA; phenological traits were days to bolting, flowering, and seed maturity averaged over sites, and flowering to bolting at CF and Pullman (PU; Washington, USA) sites; production traits were survival, leaf number, flowers per umbel, and seeds per plant averaged over sites.

nology and production traits. Given that correlations of climatic variables with PC 2 phenology and PC 2 production were less frequent than for PC 1 phenology and production (Table 4), and explained much less of the total variation (Table 3), regression models for composite phenology and production traits were completed only on PC 1 phenology and PC 1 production.

Regression models and mapping plant traits to landscape environments

Regression of environmental variables with bolting, an important phenology trait, and seeds per plant, an important production trait, produced models with R^2 values of 0.60 and 0.46, respectively (Table 5). The resulting landscape maps showed the interaction between genetic variation and source location climate for bolting and seed production (Fig. 1). The later bolting in gardens associated with generally lower temperature locations (Table 4) usually mapped to higher elevations (blue to green hues) (Fig. 1). Earlier garden bolting was typical for locations from warmer climates and was usually coupled with lower precipitation (yellow and orange hues) (Fig. 1). Higher seed production in gardens was associated with lower temperature, higher precipitation locations (green to blue hues) (Fig. 1).

Regression models between source climate and PC 1 phenology and PC 1 production had R^2 values of 0.73 and 0.52, respectively (Table 5). For PC 1 phenology, loading coefficients for bolting (0.562), days to flowering (0.445), and days to seed maturity (0.343) were all positive and strong; loadings for days from flowering to bolting at PU (−0.361) and CF (−0.488) were strong and negative. As a result, locations with high PC 1 scores for phenology were associated with later bolting dates, later flowering, and later seed maturity in gardens, but a shorter bolting to flowering period. Those higher PC 1 phenology scores, shown as blue to green hues (Fig. 1), usually mapped to the western and south-central Northern Basin and Range and the center of the Central Basin and Range. Lower PC 1 phenology scores representing warmer, drier areas (yellow to brown hues) usually mapped to the western, southern, and eastern Central Basin and Range, and the rim of the Snake River Plain (Fig. 1). The PC 1 phenology map was similar in form to

Table 4. Summary of environmental variables at source locations and their correlations with plant traits measured in common gardens for tapertip onion collected in the Great Basin (*n* = 53).

Variable or plant trait	Latitude	Longitude	Elevation (m)	Annual precipitation (mm)	Annual maximum temperature (°C)	Annual minimum temperature (°C)	Annual average temperature (°C)	Frost-free days
Mean	42.1134	−116.2861	1697	385	14.6	−0.5	7.1	95
Minimum	39.3995	−119.6893	814	252	11.2	−6.3	2.5	41
Maximum	44.9750	−114.2481	2244	792	17.1	2.7	9.4	131
Morphology								
Leaf width	−0.31*	0.10	0.27*	0.11	−0.07	0.16	0.06	0.06
Leaf length	−0.08	0.02	−0.03	−0.02	0.06	0.17	0.13	0.07
Leaf length to width	0.30*	−0.04	−0.37**	−0.14	0.14	−0.03	0.05	0.01
Scape length	−0.05	0.13	−0.05	−0.22	0.10	−0.06	0.01	−0.04
Scape diameter	−0.25	0.15	0.33*	0.17	−0.21	0.05	−0.07	−0.17
Scape length to diameter	0.18	0.00	−0.35**	−0.28*	0.23	−0.08	0.07	0.13
Umbel diameter	−0.25	−0.06	0.25	−0.01	−0.08	0.04	−0.02	−0.03
Flower color CF	−0.31*	0.07	0.32*	−0.01	−0.08	−0.04	−0.07	−0.14
PC 1 morphology	−0.28*	0.08	0.27*	0.05	−0.09	0.09	0.01	−0.04
PC 2 morphology	−0.23	−0.02	0.37**	−0.21	0.20	−0.02	0.09	0.10
Phenology								
Bolting date	−0.07	−0.06	0.33*	0.31*	−0.44**	−0.43**	−0.48**	−0.48**
Flowering date	0.07	−0.22	−0.02	0.03	−0.12	−0.28*	−0.23	−0.28*
Days bolt to flower PU	0.16	0.10	−0.46**	−0.37**	0.43**	0.20	0.33*	0.32*
Days bolt to flower CF	0.12	−0.12	−0.42**	−0.41**	0.49**	0.39**	0.48**	0.48**
Days to seed maturity	−0.07	−0.10	0.05	−0.12	0.00	−0.16	−0.10	−0.20
PC 1 phenology	−0.08	−0.08	0.33*	0.28*	−0.40**	−0.40**	−0.44**	−0.47**
PC 2 phenology	0.02	−0.12	−0.34*	−0.36**	0.33*	0.04	0.19	0.11
Production								
Emergence	0.02	0.22	0.31*	0.33*	−0.46**	−0.36**	−0.45**	−0.40**
Leaf number	0.32*	0.03	0.12	0.56**	−0.36**	−0.30*	−0.36**	−0.19
Flowers per umbel	−0.18	0.21	0.34*	0.09	−0.25	−0.17	−0.22	−0.37**
Seeds per plant	0.20	0.09	0.12	0.42**	−0.30*	−0.27*	−0.31*	−0.38**
PC 1 production	0.12	0.17	0.27*	0.43**	−0.42**	−0.34*	−0.41**	−0.42**
PC 2 production	0.37**	−0.11	−0.12	0.38**	−0.15	−0.15	−0.17	0.12

Note: *, Pearson correlation coefficients significant at $P < 0.05$; **, Pearson correlation coefficients significant at $P < 0.01$. CF, Central Ferry site, Washington; PU, Pullman site, Washington.

Table 5. Coefficients of determination (R^2) and regression equations for bolting, seeds per plant, and principal components (PC) for phenology 1 and production 1 modeled with geographic and monthly climate variables at source locations for tapertip onion.

| Trait	R^2	Regression equation
Bolting	0.60	74.5 + Feb pre (−0.175) + Mar pre (0.203) + Jan max T (−4.38) + May max T (−3.62) + Oct max T (6.32) + Mar min T (−3.75) + Dec ave T (4.69)
Seed per plant	0.46	81.4 + Jan pre (1.65) + May pre (0.809) + Oct pre (−2.40) + Dec pre (−0.705) + Jan max T (3.95) + Frost-free days (−0.350)
PC 1 phenology	0.73	−158.1 + Longitude (−0.899) + May pre (0.143) + Jun pre (−0.099) + Aug min T (−3.50) + Sep min T (6.37) + Oct min T (−3.94) + Last spring frost (0.107) + Jun ave T (−2.65) + Jul ave T (5.15) + Sep ave T (−1.90)
PC 1 production	0.52	12.347 + Jan pre (0.213) + Apr pre (0.109) + Jul pre (0.090) + Oct pre (−0.323) + Dec pre (−0.137) + First fall frost (−0.054) + elevation (0.001)

Note: Pre, precipitation; T, temperature; max, maximum; min, minimum; ave, average.

the bolting map (Fig. 1), although more area was mapped in the Central Basin and Range and less in the Snake River Plain (Fig. 1).

For PC 1 production, the loading coefficients were strong and positive for emergence (0.482), leaves per plant (0.465), flowers per umbel (0.483), and seeds per plant (0.564), indicating locations with high PC 1 production scores had higher emergence, more leaves, more flowers, and produced more seeds in common gardens. As expected, the PC 1 production map had many similarities to the seeds per plant map (Fig. 1). It did allow for additional mapped areas, especially for areas in western Utah. Higher production in gardens mapped to the higher precipitation, lower temperature areas associated with higher PC 1 production scores (blue to green hues) (Fig. 1). Except for in the north and east, the Snake River Plain was dominated by mid to lower PC 1 production scores associated with limited precipitation and relatively warm temperatures (Fig. 1). The lowest PC 1 production scores corresponded to areas with historically high temperatures and low precipitation, such as the northwestern and eastern Central Basin and Range (Fig. 1).

The overlay of PC 1 for phenology and PC 1 for production based on high, medium, and low PC categories resulted in nine proposed seed zones (Fig. 2). The majority of the mapped area was represented by six seed zones; that is, high, medium, and low phenology categories each within the medium and low production categories. In general, the medium production scores (shown as green hues) represented areas with lower temperature and higher precipitation than did low production scores (shown as yellow to brown hues). Although ecoregions have been suggested for use as provisional seed zones when genecology studies are not available (Erickson et al. 2004; Johnson et al. 2004), our results showed that Omernik level III ecoregions did not correspond with seed zones for tapertip onion based on genetic variability and source location climate. This is not surprising, considering the wide climatic variation across many ecoregions, and is consistent with genecology studies of mountain brome (*Bromus carinatus* Hook. & Arn.) (Johnson et al. 2010) and ocean spray (Horning et al. 2010).

Fig. 1. Tapertip onion maps of bolting, seeds per plant, principal component 1 (PC 1) for phenology, and PC 1 for production in relation to environmental variables over level III Omernik ecoregions. The circles show collection locations. Model predictions outside the data range for traits were not mapped and are shown in white; for PCs, that was the range between the maximum and minimum PC scores. The contours were the $\pm P = 0.05$ confidence interval, based on the regression model error.
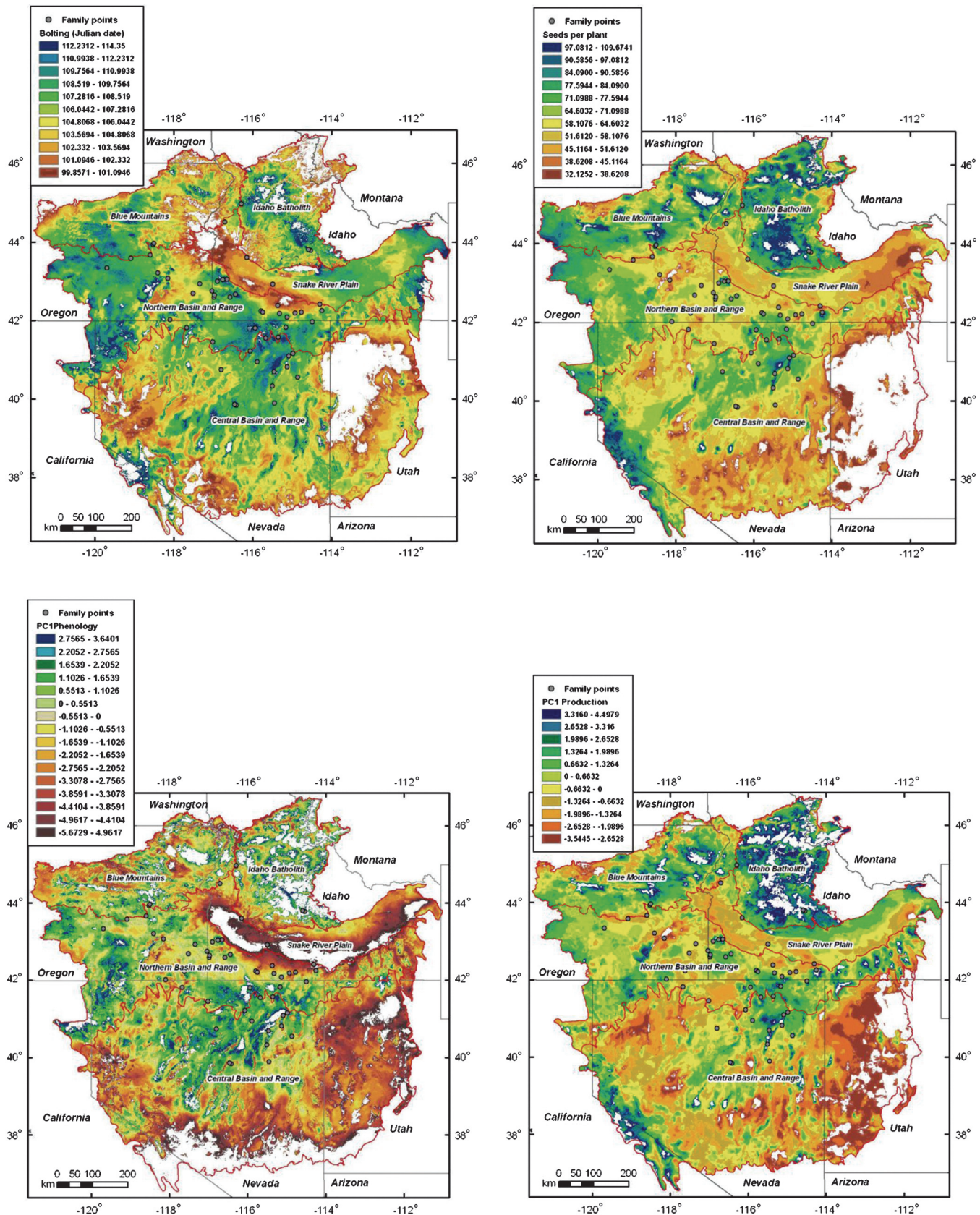
Fig. 2. Proposed seed zones for tapertip onion over level III Omernik ecoregions, based on overlays of PC 1 phenology (Phen) and PC 1 production (Prod) regression models. The circles show collection locations. The range of PC scores were divided by thirds into high, medium, and low categories and overlain to give nine seed zones. Model predictions for either PC1 phenology or PC 1 production outside the range between the maximum and minimum PC scores were not mapped and are shown in white. The contours were the $\pm P = 0.05$ confidence interval, based on the regression model error.
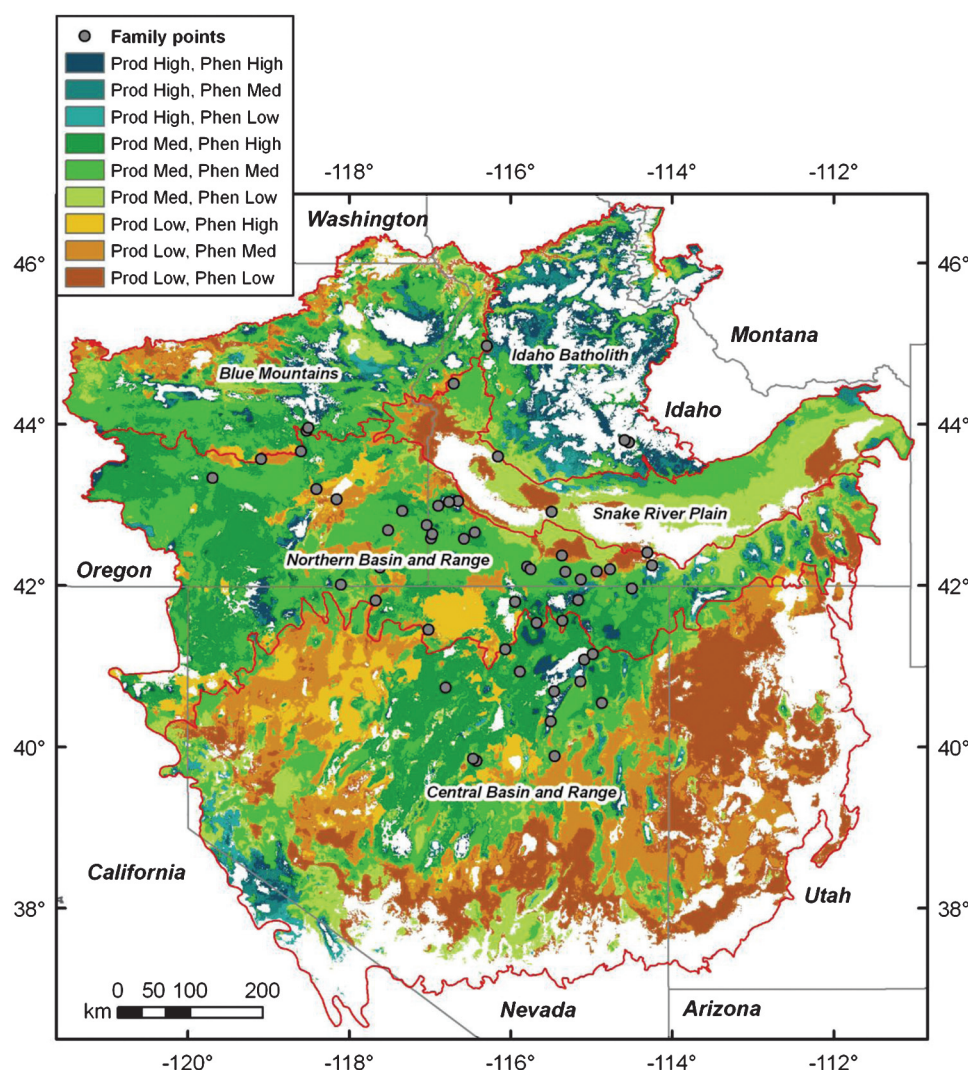
Discussion

Previous genecology studies have used a single PCA for all traits (Campbell 1986; St Clair et al. 2005; Johnson et al. 2010). Similar to Johnson et al. (2012), we initially separated traits into morphological, phenological, and production categories on which separate PCA was completed, allowing the biological meaning of each group PC to be clearly defined a priori. The PC 1 for phenology and PC 1 for production both explained the majority of the variation, and the regression of PC 1 phenology and PC 1 production with climate variables explained 74% and 50% of the variation, respectively. As a result, we concluded that the overlay of PC 1 phenology and PC 1 production, resulting in the proposed seed zones (Fig. 2), gave a strong representation of the interaction between source location climate and common garden traits.

Because areas that fell outside the observed data range were not mapped, there was some fragmentation in certain areas. This was most prominent in the Snake River Plain and the western and southern fringe of the Central Basin and Range (Fig. 2). Yet most of the collection area was mapped, providing guidance to land managers for selecting germplasm sources for restoration in the form of seeds or bulbs.

Our results are consistent with the widespread genetic variation generally observed in common garden research (Galloway and Fenster 2000; Hufford and Mazer 2003; Kawecki and Ebert 2004; St Clair et al. 2005; Leimu and Fischer 2008; Bischoff et al. 2010; Horning et al. 2010; Johnson et al. 2010, 2012). Although exceptions have accumulated (Galloway and Fenster 2000; Leimu and Fischer 2008; Bischoff et al. 2010; Hancock et al. 2012), locally derived germplasm has often been shown to have an adaptive advantage (Hufford and Mazer 2003, Rice and Knapp 2008, Leimu and Fischer 2008). Another key to successful restoration is population diversity, as emphasized by Leimu and Fischer (2008) and Bischoff et al. (2010). Thus, the use of diverse germplasm sources guided by seed zones has the advantage of providing genetic variation across the landscape to advance in situ conservation and the potential for future natural selection and evolution. Given that long-term climate differences were linked with genetic variation in phenology and production traits, resulting in strong regression models, our results suggest that natural selection and adaptation were

important factors driving differences in garden traits among source locations (Endler 1986; Kawecki and Ebert 2004).

Still, plasticity and genetic variation interact to modify a given phenotype in a given environment (Falconer 1981; Scheiner and Goodnight 1984; Schlichting 1986; Roach and Wulff 1987; Sultan 2000; Galloway and Etterson 2007; Herman and Sultan 2011). For example, phenology was later at the cooler PU garden site in response to lower temperatures than at the CF site, a plastic response. Within gardens at both sites, plants from cooler locations had generally later phenology, showing genetic variation associated with source location climates (Table 2). We would expect that at progressively colder climates, the genetic potential for later development and higher seed production observed for colder locations in common gardens would be dampened by short, low temperature conditions during reproductive development. Although not predictive of phenotypes for a given year and location in situ, the genecology approach is a direct assessment of the interaction of genetic variation and long-term source location climate, making it effective for seed zone delineation.

Nevertheless, for a direct assessment of adaptation, reciprocal transplant studies are recommended. Although impractical at all 53 source locations, they could be approached using the seed zone framework to extract a smaller, focused germplasm set for evaluation. For example, germplasm from high and low production and phenology zones could be contrasted. This would still be challenging, given the need for a long-term approach and assessment of the relative contributions of seeds and bulbs to survival and fecundity (Phillips 2010). Pinpointing adaptive responses in contrasting environments would help to verify and modify seed zones and provide insight into tapertip onion survival, fecundity, and evolution.

Developing seed zones is necessarily based on some subjectivity, so the maps should be considered as tools to guide restoration and management, rather than rigid units. For example, the contour intervals for the PC 1 phenology and PC 1 production (Fig. 1) were based on the $\pm P = 0.05$ confidence interval. A confidence interval of $P = 0.01$ would have resulted in wider contours and less detail; a contour of $P = 0.10$, narrower contours and more detail. Modification of trait maps and seed zones with more or less detail may be desired by restoration practitioners, based on management considerations and experience. Changes to the contour intervals or seed zone number would not change the regression models; the basic form of the relationship between genetic variability and climate would remain intact.

Except for bulb survival, this research examined the interaction of genetic traits with source climate beyond the establishment phase. Restoration with bulbs has some advantages over seeds (Hellier and Johnson 2010), but the emergence and survival of bulbs or seeds at specific source locations needs to be tested. This study indicated that beyond establishment, phenology and production traits interacted with climate to reveal differences associated with climate variation that are potentially adaptive.

Given the potential for year by site interactions, especially at somewhat higher P values than $P < 0.01$ (Table 2), interactions would not be unexpected at diverse year and site combinations across the study area. Thus seed zone development using additional data could modify their shape and size. Moreover, the climate data used for modeling PCs are historic, and the expectation is that climate change will affect the distribution of tapertip onion and other species. However, the garden data also provide an opportunity to examine tapertip onion distribution under different climate change scenarios. Even with the need for verification and potential modifications, the proposed seed zones map was based on relatively strong connections between traits and location climates, suggesting the basic outline for seed zones was established.

Although wide adaptation may be possible by selection or breeding of native germplasm cultivars with specific attributes (Jones and Young 2005), potential drawbacks include genetic swamping (Hufford and Mazer 2003; Johnson et al. 2010), outbreeding depression (Kramer and Havens 2009), hybridization that may lead to the loss of coadapted gene complexes and unfavorable interactions with other plant and animal species. Populations with high growth potential may be more competitive and easier to establish (Hancock et al. 2012) but are not necessarily the most suitable when conservation of germplasm in situ and interactions with other species are considered. In many regions, there is accelerating pressure on species population diversity, intensified by past restoration with exotic species and use of single or limited germplasm sources that may contribute to genetic erosion (Hufford and Mazer 2003). With this comes the potential loss of species genetic variation, emphasizing the need for collection and maintenance of populations ex situ (Merritt and Dixon 2011).

Because the scope for future selective adaption depends on the availability of genetic variation, we recommend numerous wild populations be collected and used for restoration within seed zones to obviate those concerns. Collections that focus on certain restoration sites with unusual attributes such as microclimate or soil type may also be needed within seed zones. We expect other herbaceous species to show patterns of genetic variation linked to climatic variables, and similar genecology studies on other key species are needed to help conserve and utilize genetic variation now into the future.

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