

Genecology of *Holodiscus discolor* (Rosaceae) in the Pacific Northwest, U.S.A.

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Abstract

An important goal for land managers is the incorporation of appropriate (e.g., locally adapted and genetically diverse) plant materials in restoration and revegetation activities. To identify these materials, researchers need to characterize the variability in essential traits in natural populations and determine how they are related to environmental conditions. This common garden study was implemented to characterize the variability in growth and phenological traits relative to climatic and geographic variables of 39 *Holodiscus discolor* (Pursh) Maxim. accessions from locations throughout the Pacific Northwest, U.S.A. Principal component analysis of 12 growth and phenological traits explained 48.2% of the observed vari-

ability in the first principal component (PC-1). With multiple regressions, PC-1 was compared to environmental values at each source location. Regression analysis identified a four-variable model containing elevation, minimum January temperature, maximum October temperature, and February precipitation that explained 86% of the variability in PC-1 ($r^2 = 0.86$, $p < 0.0001$). Spatial analysis using this regression model identified patterns of genetic diversity within the Pacific Northwest that can help guide germplasm selection (i.e., seed collections) for restoration and revegetation activities.

Key words: common garden, genecology, germplasm, *Holodiscus discolor*, Oceanspray.

Introduction

In recent years, land managers have increasingly focused attention on the use of native plant species in habitat restoration and land reclamation activities (Booth & Jones 2001; Hufford & Mazer 2003). Moreover, management agencies have been striving to use locally adapted materials rather than commercially produced cultivars of native species, especially if the cultivars are seen as highly bred or from a genetically narrow base (Lesica & Allendorf 1999; Hufford & Mazer 2003; Rogers & Montalvo 2004). Unfortunately, formal guidelines on how to develop locally adapted releases for a given species in the wild do not exist for many native plant species (Johnson et al. 2004). To identify plant movement guidelines (e.g., seed zones), researchers first need to quantify the phenotypic genetic variation found in a species within a geographic region of interest (e.g., species range, management area; Hufford & Mazer 2003; Johnson et al. 2004). Patterns of genetic variation vary by species (i.e., generalist vs. spe-

cialist) and by region; consequently, plant movement guidelines are determined on a species-by-species basis. Historically, this approach was developed for forest tree species (Campbell & Sorensen 1978; Rehfeldt 1978; Johnson et al. 2004) and has more recently been successfully applied on nontimber native plant species (Erickson et al. 2004; Doede 2005).

One important restoration species, Oceanspray (*Holodiscus discolor* (Pursh) Maxim.), is a multistemmed roseaceous shrub that is distributed throughout the Pacific Northwest from British Columbia, Canada, to southwestern California, U.S.A. This showy understory shrub is dominant in many forest communities at elevations from sea level to approximately 2,500 m. *Holodiscus discolor* is a tetraploid ($2X = n = 18$; Goldblatt 1979; McArthur & Sanderson 1985; Antieau 1986), and there are no published accounts of population-level ploidy variation. Moreover, given the significant partitioning of phenotypic variation among locations observed in this study (see below), variation in ploidy may not be common in *H. discolor* in the Pacific Northwest; however, additional studies would be needed to confirm this. Preliminary common garden results indicate that there is substantial genetic variation in characters such as growth habit, growth rate, leaf morphology, and flower abundance (Flessner et al. 1992). *Holodiscus discolor* can readily occupy a broad range of habitat types, grows vigorously, and is an important browse for large game animals (e.g., deer, elk; Flessner et al. 1992). Given these characteristics, *H. discolor* is used in a variety of small-scale revegetation projects

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including streamside and road cut revegetation and conservation plantings throughout the Pacific Northwest (Antieau 1987; Flessner et al. 1992). Although the spatial scope of most projects that use *H. discolor* is not extensive, this species is considered valuable in restoration efforts, and there is a demand for germplasm for both private and wildland applications. Consequently, there is a need to identify appropriate germplasm sources for use in revegetation activities.

To ensure locally adapted seed sources of *H. discolor* for use in the Pacific Northwest region of the United States, we need to understand how variation in phenotypic traits relates to key environmental factors. In this study, we used a genecological approach to characterize phenotypic genetic variation expressed by *H. discolor* relative to climatic and geographic variables throughout the Pacific Northwest by analyzing a common garden study originally conducted to document genetic differences and make ecotypic selections. The results of this study are being used to modify and guide seed source selection for United States Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) germplasm releases for *H. discolor* and, more broadly, can provide seed movement recommendations to assist land managers when creating essential germplasm collections for habitat restoration.

Methods

Seed Collection and Common Garden Design

As part of an earlier study initiated in 1987, bulk seed collections from multiple parent plants were initially made at 45 source localities (i.e., accessions) representing a variety of *Holodiscus discolor* habitats throughout the Pacific Northwest, including northern California, Oregon, and Washington. Viable seed was collected from two to six maternal plants separated by 5–30 m at each source locality. *Holodiscus discolor* has a naturally patchy distribution and populations are often small; consequently, seed collections for this study often represent a substantial proportion of the individuals growing at a given site. This current reanalysis is based on 39 of the original 45 collections (Fig. 3). Complete seed germination and seedling estab-

lishment procedures and common garden design and layout are described in Flessner et al. 1992. Seed lots were cold stratified and germinated in a greenhouse. The seedlings were overwintered and in 1989 used to establish a single-site common garden at the USDA NRCS, Corvallis Plant Materials Center, Corvallis, Oregon. Four-plant row plots were replicated up to five times (based on available seed) in a randomized design.

Trait Measurement

From 1990 to 1996, measurements and observations were collected on a suite of morphological and phenological characters (Table 1). Plant height and canopy width were directly measured on individual plants. Additionally, stem density, vigor, foliage appearance (an assessment of damage from insect herbivory and disease symptoms), flower abundance, and date of budbreak (Julian date) were visually scored (Table 1). Climate data for each location were generated using PRISM (Parameter Elevation Regressions on Independent Slopes Model; PRISM Group; PRISM Group, Oregon State University 2007). For a 4 × 4-km grid centered on given latitude and longitude (i.e., collection site), this model estimates mean annual and monthly precipitation and temperature, mean minimum and maximum monthly temperature, and the mean dates of the last and first frost (i.e., number of frost-free days).

Statistical Approach and Analyses

All statistical analyses were performed with the SAS statistical software package (SAS Institute Inc. 1999). Only accessions with at least seven observations remaining in the garden at the end of the 1990 growing season were included in the statistical analyses resulting in a total of 39 accessions analyzed. Under-representation in garden plots was not a function of low survivorship in the plantings but, rather, a lack of viable seed for planting fully replicated plots. Consequently, some accessions with limited representation were dropped from this current analysis. Analysis of variance (ANOVA) (PROC MIXED) was conducted on all traits to identify statistical differences between accessions. For this initial ANOVA, analyses of 15 traits were conducted on individual plant values. A subset of

Table 1. Growth and phenological traits and their measurements.

Trait	Measurement/Observation	Abbreviations	Year(s) Measured/Observed
Canopy width	Greatest width of canopy (cm)	cwYEAR	1990, 1991, 1992
Shrub height	Greatest height of shrub (cm)	htYEAR	1990, 1991, 1992
Height growth increments	Height (cm) year 2 – height (cm) year 1	htYEAR1_htYEAR2	1991, 1992
Height, canopy width ratio	Height (cm)/canopy width (cm)	htcw_ratYEAR	1990, 1991, 1992
Stem density	Scored 1–9	sdYEAR	1990, 1992
Abundance of flowering	Scored 1–9	flrYEAR	1991, 1992
Apparent pest damage	Scored 1–9	pestsYEAR	1990, 1991, 1992, 1993
Vigor	Scored 1–9	vigorYEAR	1990, 1991, 1992
Date of budbreak	Date when ≥75% of buds open	budbreakYEAR	1991, 1995

traits were originally scored by plot (budbreak91, budbreak95, flr92, pests91-93, sd92, and vior91-92); consequently, analyses were conducted on plot means. Of the 24 traits analyzed, 18 that exhibited significant variation ($p < 0.05$) were examined in further analyses. All subsequent analyses for all traits were conducted on accession means. Correlations among traits were analyzed to determine colinearity, and consequently, 12 traits were retained for final analysis (Table 2). Correlations to environmental variables were determined for these 12 traits (Appendix). Principal component analysis (PROC PRINCOMP) was conducted on the remaining 12 traits to better capture the location variation with a smaller set of unique variables (i.e., components). Because the first principal component (PC-1) explained a large amount of the variation in the dataset, it was the only variable considered in further analyses. The environmental variables of interest extracted from PRISM for each site were as follows: latitude, longitude, elevation, slope, fall first frost day, spring last frost day, total annual frost-free days, annual amount of precipitation, average annual temperature, minimum monthly precipitation, maximum monthly precipitation, minimum monthly temperature, and maximum monthly temperature. Simple and multiple regression models were constructed by regressing PC-1 and geographic and climatic variables. Model building was performed by using the r^2 selection method of the PROC REG procedure that identifies the models with the largest regression coefficient

of determination (r^2) for the specific number of variables considered.

We used Spatial Analyst in ArcGIS version 8.3 (ESRI, Redlands, CA, U.S.A.) to map predicted patterns of genetic diversity on the landscape as calculated by our regression model. Using an objective classification scheme based on standard deviations about the mean, contour intervals were classified from the range of calculated values generated by the model (i.e., values for PC-1) within the western Pacific Northwest. We chose this classification scheme over others (e.g., Jenks, user-defined intervals) because it required minimal subjective input to define the number of intervals. Contour intervals bounded each of the three standard deviations above and below the mean in addition to the mean for a total of seven contour intervals, each with an interval size of one standard deviation.

Results

Of the 24 traits initially analyzed via ANOVA, 18 showed statistically significant differences ($p < 0.05$) among accessions; 6 did not show significant differences and were eliminated from the analysis (Table 2). An investigation of the correlation among traits revealed colinearity involving a subset of seven traits. Six (cw91, ht91, ht92, vigor90, vigor91, and vigor92) were eliminated, leaving 12 traits for further analyses (Table 2). These traits were correlated with a variety of environmental variables (Appendix). In general, most statistically significant ($p < 0.5$) correlations occurred with monthly minimum temperature values (Appendix).

Principal component analysis revealed that principal component 1 explained 48.2% of the variation in the data (eigenvalue = 5.78). Principal components 2 and 3 had eigenvalues close to 1 and only explained a small proportion of the variability (11.8 and 9.7%, respectively). Consequently, only PC-1 was retained for further analysis as a representation of growth and phenological traits for *Holodiscus discolor* (Table 3).

Table 2. Results of ANOVA on 24 growth and phenological traits among 39 accessions *Holodiscus discolor*.

Trait	Trait Mean	CV	F	p
budbreak91	51.91	2.48	6.78	0.0001
budbreak95	104.22	4.61	13.57	0.0001
cw90	73.56	27.38	6.22	0.0001
cw91	116.03	20.79	7.49	0.0001 ^a
cw92	132.00	17.09	4.27	0.0001
flr91	3.70	87.82	2.31	0.0003
flr92	5.25	19.51	8.08	0.0001
ht90	101.23	18.90	12.76	0.0001
ht91	128.91	16.89	11.68	0.0001
ht91_90	27.96	68.68	1.63	0.0221
ht92	152.64	14.44	8.68	0.0001 ^a
ht92_91	23.72	77.38	1.03	0.4329 ^b
htcw_rat90	1.50	33.77	1.13	0.3039 ^b
htcw_rat91	1.16	24.66	1.16	0.2685 ^b
htcw_rat92	1.20	19.28	1.27	0.1647 ^b
pests90	4.11	25.21	1.87	0.0051
pests91	3.52	27.29	1.23	0.1935 ^b
pests92	4.71	17.56	1.29	0.1463 ^b
pests93	4.31	21.13	3.51	0.0001
sd90	3.53	41.89	6.37	0.0001
sd92	4.02	21.86	2.97	0.0001
vigor90	2.63	39.44	7.73	0.0001 ^a
vigor91	3.35	21.43	6.02	0.0001 ^a
vigor92	3.05	25.85	5.49	0.0001 ^a

Traits in bold were retained for further analysis. CV, coefficient of variation.

^a Trait dropped due to colinearity.

^b Trait dropped due to nonsignificance ($p < 0.05$) in ANOVA.

Table 3. Correlation coefficients (r) for PC-1 and *Holodiscus discolor* growth and phenological traits.

Trait	r
cw90	-0.91
cw92	-0.89
flr91	-0.13
flr92	0.78
ht90	-0.93
ht91_90	-0.47
pests90	0.37
pests93	0.63
budbreak91	0.75
budbreak95	0.69
sd90	0.89
sd92	0.30

Significance levels are $r_{0.10} = 0.19$, $r_{0.05} = 0.31$, $r_{0.01} = 0.41$, $r_{0.001} = 0.51$, and $r_{0.0001} = 0.58$.

Correlation analysis between PC-1 and geographic and climatic variables revealed significant patterns (Table 4; Fig. 1). Overall, PC-1 was only weakly correlated with monthly precipitation, monthly maximum temperatures, annual precipitation, annual average temperature, and geographic location (except elevation). PC-1 was strongly negatively correlated with minimum monthly temperatures, first frost in fall, and total frost-free days. PC-1 was strongly positively correlated with the last frost in spring and elevation.

Regression analysis indicated that both geographic and climatic variables contributed to the variability in growth and phenological characters (PC-1). An exploration of potential models revealed that a single-parameter model with elevation explained a substantial amount of the observed variability ($r^2 = 0.63$, $F = 63.88$, $p < 0.0001$; Fig. 2). Of the multiple-parameter models, a four-parameter model composed of elevation, minimum January temperature, maximum October temperature, and February precipitation explained significantly more of the observed variability ($r^2 = 0.86$, $F = 53.02$, $p < 0.0001$).

$$\begin{aligned} \text{PC-1} = & (0.002 \times \text{Elevation}) \\ & - (0.80 \times \text{Minimum January Temperature}) \\ & + (0.56 \times \text{Maximum October Temperature}) \\ & + (0.01 \times \text{February Precipitation}). \end{aligned}$$

Table 4. Correlation coefficients (r) for environmental variables and principal component axis 1 (growth and phenology).

Month	Minimum Temperature	Maximum Temperature	Precipitation
January	-0.6442	-0.4828	0.169
February	-0.6608	-0.4514	0.1847
March	-0.6651	-0.4327	0.175
April	-0.711	-0.4071	0.1474
May	-0.7181	-0.274	0.1521
June	-0.7361	-0.063	0.0137
July	-0.6437	0.2338	-0.1916
August	-0.679	0.2607	-0.2115
September	-0.6381	0.1926	-0.0371
October	-0.66	-0.1559	0.0683
November	-0.6668	-0.4952	0.2356
December	-0.6489	-0.5153	0.1722
Annual	—	—	0.163
Additional variables			
Latitude	-0.3787		
Longitude	0.3509		
Elevation (m)	0.7958		
Slope	0.1126		
First fall frost	-0.6431		
Last spring frost	0.672		
Total frost-free days	-0.6679		
Annual average temperature	-0.5053		

Significance levels are $r_{0.10} = 0.19$, $r_{0.05} = 0.31$, $r_{0.01} = 0.41$, $r_{0.001} = 0.51$, and $r_{0.0001} = 0.58$.

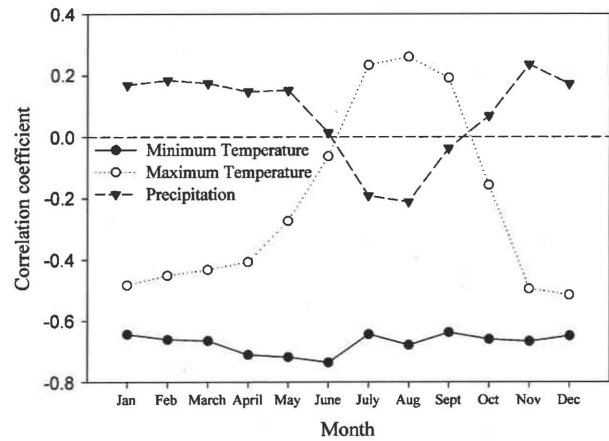


Figure 1. Correlation coefficients (r) of PC-1 score and key climatic variables (e.g., minimum and maximum monthly temperatures and monthly precipitation).

Other complex multiple-parameter models (i.e., more than four terms) failed to significantly increase the amount of explained variability. To use a model that is biologically meaningful and practical for land management activities, we chose the aforementioned four-term model.

Using the regression model with the elevation and climatic variables generated by PRISM, we generated a map of predicted PC-1 values for *H. discolor* in the Pacific Northwest (Fig. 3). Predicted PC-1 values range from approximately -7.1 to 13.4 and are divided into seven contour intervals. Two PC-1 contour intervals (8.57–11.56 and 11.56–13.39) encompassed *extremely* small geographic areas in northern Washington. Consequently, on the predictive map, these two contour intervals were combined with contour interval 5.57–8.57 to create one larger contour interval 5.57–13.39 for a total of five displayed contour intervals (Fig. 3). For clarification, this map also shows the 39 accessions included in this current study and

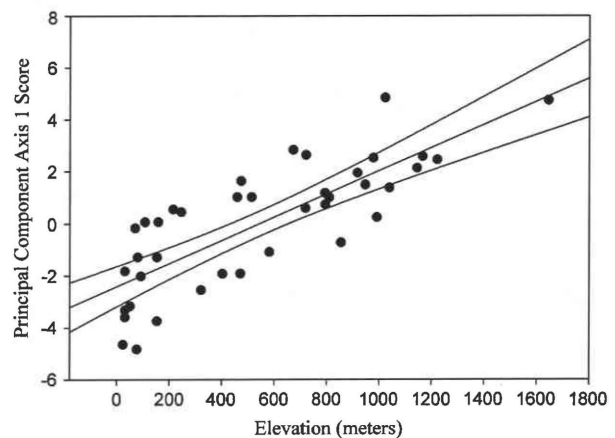


Figure 2. Regression of PC-1 score and elevation with 95% confidence intervals; $r^2 = 0.63$, $F = 63.88$, $p < 0.0001$.

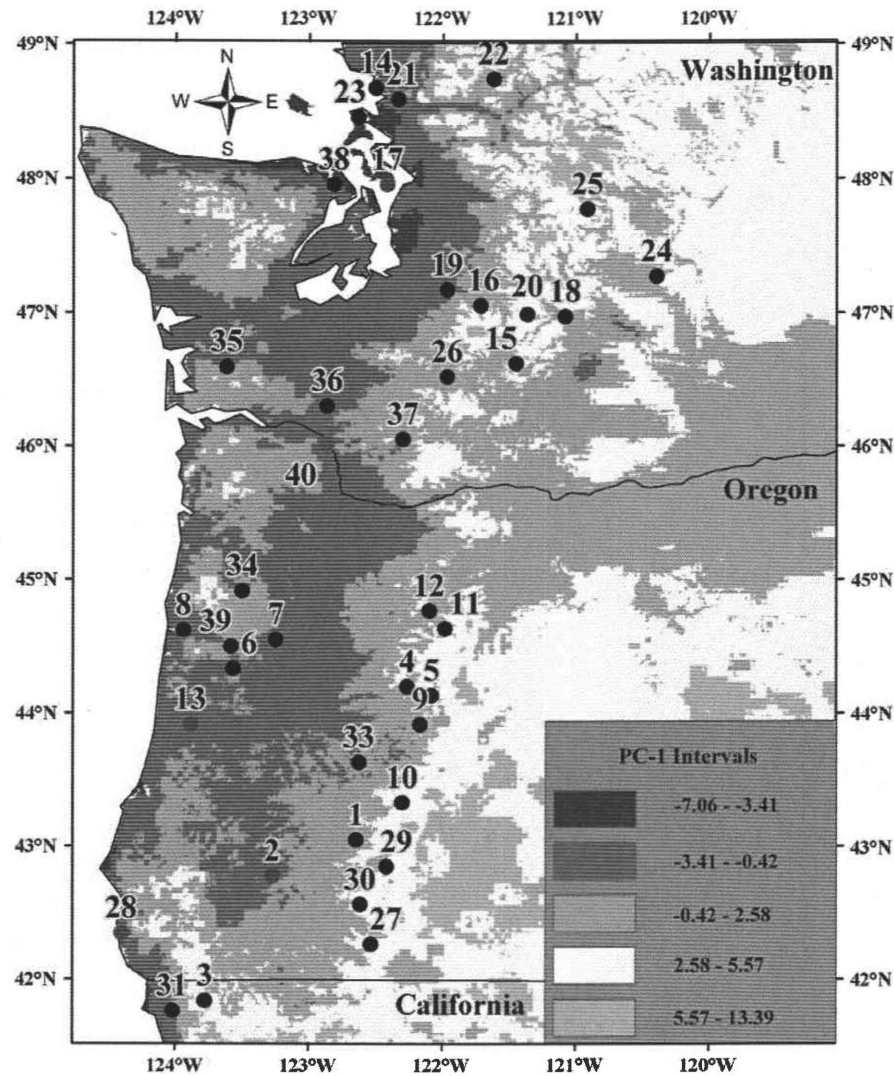


Figure 3. Map of predicted PC-1 values for *Holodiscus discolor* in the Pacific Northwest as calculated using the four-parameter regression model of elevation and climatic variables. Color shades represent contour intervals (i.e., regions of genetic similarity) for PC-1 values as determined by the range of calculated values. The 39 locations of *H. discolor* accessions are shown for reference. Four locations shown in red identify accessions that were selected to propagate germplasm sources in 1996. The single location shown in blue was selected as a germplasm source in 1996 but was eliminated from this current analysis.

the subset of five accessions (one of which was dropped from the current analysis) that were previously selected as part of an earlier study (Flessner et al. 1992) in 1996 based on overall performance to create isolated seed orchards for germplasm release.

Discussion

Original Study Design and Current Genecological Analysis

The design of the original study differs from typical genecological study designs in several respects (Johnson et al. 2004). For example, in some U.S. studies, population sam-

pling is usually denser over the geographic range of interest but with fewer parents per location (Campbell 1991; Sorensen et al. 2001; Erickson et al. 2004). On the other hand, some Canadian examples from British Columbia and Mexico typically sample a similar number of populations but have more parents per population and multiple test sites (Ying 1997; Sáenz-Romero et al. 2006). However, these differences do not prohibit using the genecological approach to analyze the common garden data. In this analysis, *Holodiscus discolor* exhibited highly significant phenotypic differences even with a relatively coarse level of population sampling. In this analysis, seed samples at each location were bulked rather than maintained by

family, and therefore, we cannot quantify the heritability of the traits we are examining nor are we able to quantify the level of within-population variation; neither of these products are essential to the goals of this study. Finally, this common garden study was deployed at a single site rather than being replicated at contrasting sites. Studies examining genotype $\times$ environment effects (i.e., $G \times E$, including some genecological studies) require contrasting environments to detect variable responses in a given trait. We are simply looking for among-site differences and not a $G \times E$ effect; therefore, this one site allowed us to detect these differences.

Genetic Diversity Relative to Environmental Variables

Our results indicate significant source variation in a variety of growth and phenological traits of *H. discolor*. These traits are correlated with a suite of environmental variables but predominantly with minimum temperature and associated variables (e.g., frost-free period). Moreover, an analysis of mesic and xeric sites (as defined by aspect data for each site) indicates that although these two classes have similar slopes when regressed against PC-1 ($F = 0.77$, $p = 0.3868$), they have slightly different intercepts (data not shown). Possibly, *H. discolor* may respond to microclimate conditions, but given the minimal differences revealed in our analysis, we do not feel that these warrant inclusion in management applications. However, these results indicate that the *H. discolor* is a habitat specialist rather than a generalist and that germplasm should not be moved throughout its range. Additionally, the germplasm collections currently under development are insufficient to represent the broad array of potential planting sites, and more genetically appropriate germplasm sources need to be identified (see below).

Implications for Past Germplasm Selections

When no existing genetic data exist for a given species of interest, Environmental Protection Agency (EPA) ecoregions are sometimes used as an initial proxy for seed movement guidelines (Jones 2005). In 1996, the Corvallis Plant Materials Center selected five accessions using the ecoregion approach to develop regional germplasm releases for the western Pacific Northwest. The goal of the original project was to identify and select the "best performing" germplasm within an ecoregion that could be propagated and used as an eventual germplasm release for restoration. These accessions were selected based on how they ranked among all accessions in a given ecoregion for each trait measured (i.e., tallest, most vigorous, least pest damage). The best performing (i.e., highest ranking overall for all traits measured) accession from each of the five EPA level III ecoregions within the service district boundaries was chosen to propagate isolated seed orchards

(Darris & McGovern, unpublished data). Five seed orchards were created from self-pollinated seed collected from surviving individuals for the five selected accessions in the common garden study. Depending on survivorship, two seedlings from up to 20 genetically unique individuals were planted in two replicates in each orchard (40 individuals total). Orchards were established in isolation with 0.4–17 km of separation among orchards (one orchard per accession, five orchards total). Based on the results of the current genecological analysis and the potentially narrow genetic composition of the propagated selections, we suggest that significant modifications be made to the current germplasm collections (see below).

In the case of *H. discolor*, using the ecoregion approach yielded different results than the genecological approach of the current analysis. In some instances, the ecoregion approach correctly sampled genetic diversity. In others, it created redundant samples or failed to sample unique genetic resources. Certain genetic regions are not represented by the accessions chosen for the 1996 selections, and certain accessions included in the 1996 selections are redundant samples of the same genetic zone. Moreover, in the current analysis, even though there were significant differences among accessions from different ecoregions ($F = 3.36$, $p < 0.02$), ecoregions only explained a small proportion of the variation among accessions ($r^2 = 0.24$, $p < 0.0001$). The apparent reason for this is because ecoregions are based on a variety of climatic, environmental, and vegetative properties (McMahon et al. 2001), although minimum temperature is the primary driver of adaptive variation. Additionally, one accession that was previously selected as a release for the Willamette Valley ecoregion (accession number 17) was eliminated from this analysis due to too few replicates in the common garden.

Applications for Germplasm Management

Based on the results of this genecological analysis, modifications and additions are suggested for the existing suite of *H. discolor* germplasm selections for increase, field testing, and eventual release for restoration and revegetation activities. The selection based on accession number 17 will remain in the modified germplasm collection for the Puget Trough (PC-1 contour interval -7.1 to -3.4). However, this collection originates from a single site, and we caution that it may be best used in restoration activities in combination with additional seed collected from other locations within this contour interval (see below). The four collections based on accession numbers 2, 13, 28, and 40 for the Coast Range, Cascade Mountains in Oregon, Klamath Mountains, and Willamette Valley, respectively, should be combined and maintained as a single release for the lower elevation genetic cline (PC-1 contour interval -3.4 to -0.4). This newly combined collection will have originated from up to 60 unique genotypes from four geographically widespread populations and therefore most

likely contains an adequate sample of genetic diversity that is appropriate for limited restoration applications (Rogers & Montalvo 2004). Furthermore, this analysis has exposed new gaps in coverage not present under the previously used ecoregion approach. It suggests that recollection and additional selections would be appropriate in Washington and Oregon for the lower elevation "west slope Cascades" (PC-1 contour interval -0.42 to 2.58) and for the "east slope Cascades" (PC-1 contour interval 2.58–5.57). In short, work on two germplasm releases should proceed, and two new additional ones are needed for maximum genetically appropriate coverage. If fully implemented, these four proposed selections would represent the largest genetic clines that are present in the Corvallis Plant Materials Center service area.

This study provides essential genetic information for the development, management, and deployment of *H. discolor* germplasm in the Pacific Northwest. With these data, certain existing collections will be kept and modified, and new collections or recollections should be made to better represent the pattern of genetic differentiation on the landscape. This will help ensure the most genetically appropriate germplasm collections for restoration and revegetation activities throughout the region that are in agreement with widely accepted guidelines (Rogers & Montalvo 2004).

Guidelines for Land Managers and Future Germplasm Collections

This predictive map should prove useful for identifying areas that should be targeted for seed collection by land managers who are interested in incorporating genetically appropriate *H. discolor* sources in restoration activities. To restore a site that lies within a certain genetic interval on the map, land managers should collect seed from *H. discolor* populations that also lie within the same interval to ensure the application of appropriate germplasm. Moreover, land managers should collect seed from multiple populations and multiple maternal sources within a population to create a genetically diverse collection (Rogers & Montalvo 2004).

Additionally, this study highlights the value of genecological analyses in native plant restoration research. Specifically, we now have a case study comparing the results of the broadly applied ecoregion and genecological approaches. We believe the ecoregion approach is still valuable, especially as an initial survey of genetic variation on the landscape when no relevant genetic data exist for a given species of interest. However, as reported here, this approach has limitations when trying to identify genetic resources for wildland restoration. The genecological approach applied here (and by others elsewhere) has been successfully incorporated into management guidelines and should continue to be broadly used on native plants in the future.

Implications for Practice

- The results of this study are being used to guide the creation of locally adapted germplasm releases for *Holodiscus discolor* in the Pacific Northwest, U.S.A
- The predictive map provided in this study can be used by land managers to guide seed collection activities to ensure incorporation of genetically appropriate materials into future restoration activities.
- This study highlights the broad utility of the genecological approach for identifying appropriate genetic resources for revegetation and habitat restoration.

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Appendix . Correlation coefficients (*r*) of *Holodiscus discolor* traits measured in this study and environmental variables.

	Traits											
	<i>cw90</i>	<i>cw92</i>	<i>ftr91</i>	<i>ftr92</i>	<i>ht90</i>	<i>ht91_90</i>	<i>budbreak91</i>	<i>budbreak95</i>	<i>pests90</i>	<i>pests93</i>	<i>sd90</i>	<i>sd92</i>
Latitude	0.33	0.36	0.07	−0.32	0.44	0.17	−0.21	−0.40	−0.37	−0.05	−0.19	−0.17
Longitude	−0.32	−0.24	0.12	0.16	−0.25	−0.10	0.38	0.15	−0.09	0.47	0.54	0.04
Elevation (m)	−0.70	−0.68	−0.08	0.77	−0.81	−0.39	0.54	0.48	0.39	0.47	0.72	0.03
Slope	−0.08	0.05	0.13	0.05	−0.06	−0.18	0.20	0.03	0.36	−0.05	0.13	0.22
First fall frost	0.52	0.49	−0.21	−0.46	0.53	0.28	−0.58	−0.36	−0.10	−0.67	−0.75	−0.13
Last spring frost	−0.52	−0.53	0.20	0.54	−0.57	−0.32	0.58	0.35	0.16	0.67	0.73	0.15
Total frost-free days	0.53	0.52	−0.21	−0.51	0.56	0.31	−0.59	−0.36	−0.14	−0.68	−0.75	−0.14
Annual precipitation	−0.15	−0.11	0.01	0.13	−0.07	−0.29	0.14	0.27	0.36	−0.19	−0.01	0.37
Annual average temperature	0.44	0.40	−0.12	−0.45	0.43	0.29	−0.38	−0.18	−0.08	−0.52	−0.60	0.03
Minimum monthly temperatures												
January	0.57	0.52	−0.07	−0.53	0.57	0.33	−0.51	−0.32	−0.04	−0.58	−0.73	−0.06
February	0.57	0.53	−0.11	−0.53	0.58	0.34	−0.53	−0.34	−0.08	−0.61	−0.75	−0.05
March	0.58	0.55	−0.11	−0.55	0.59	0.35	−0.51	−0.32	−0.10	−0.60	−0.75	−0.06
April	0.60	0.58	−0.11	−0.59	0.64	0.37	−0.54	−0.39	−0.18	−0.62	−0.77	−0.07
May	0.59	0.58	−0.11	−0.61	0.64	0.38	−0.54	−0.41	−0.23	−0.63	−0.75	−0.07
June	0.61	0.63	−0.07	−0.65	0.67	0.40	−0.54	−0.40	−0.23	−0.63	−0.74	−0.04
July	0.51	0.56	−0.09	−0.60	0.52	0.42	−0.51	−0.33	−0.16	−0.57	−0.66	−0.01
August	0.56	0.61	−0.05	−0.62	0.56	0.44	−0.53	−0.35	−0.15	−0.57	−0.68	−0.02
September	0.53	0.55	−0.07	−0.59	0.53	0.39	−0.53	−0.30	−0.09	−0.54	−0.66	−0.03
October	0.57	0.56	−0.06	−0.57	0.57	0.38	−0.54	−0.30	−0.04	−0.60	−0.73	−0.01
November	0.57	0.55	−0.14	−0.53	0.58	0.40	−0.53	−0.34	−0.10	−0.62	−0.75	−0.05
December	0.56	0.53	−0.09	−0.53	0.58	0.33	−0.50	−0.32	−0.04	−0.61	−0.74	−0.04
Maximum monthly temperatures												
January	0.43	0.36	−0.10	−0.39	0.39	0.20	−0.41	−0.18	0.02	−0.53	−0.63	−0.04
February	0.39	0.33	−0.16	−0.38	0.37	0.21	−0.37	−0.16	−0.02	−0.51	−0.59	−0.03
March	0.38	0.32	−0.15	−0.39	0.37	0.24	−0.31	−0.14	−0.09	−0.46	−0.54	0.03
April	0.35	0.30	−0.13	−0.38	0.37	0.23	−0.25	−0.15	−0.15	−0.44	−0.49	0.09
May	0.23	0.21	−0.09	−0.31	0.28	0.14	−0.12	−0.01	−0.15	−0.34	−0.35	0.16
June	0.07	0.04	−0.07	−0.15	0.09	0.05	0.06	0.16	−0.09	−0.19	−0.14	0.24
July	−0.19	−0.20	−0.06	0.08	−0.21	−0.05	0.29	0.36	0.00	0.03	0.16	0.29
August	−0.18	−0.21	−0.06	0.12	−0.26	−0.03	0.31	0.36	0.01	0.08	0.21	0.27
September	−0.14	−0.20	−0.15	0.10	−0.24	0.03	0.16	0.31	0.08	0.00	0.08	0.20
October	0.15	0.10	−0.15	−0.14	0.08	0.13	−0.12	0.07	0.08	−0.33	−0.29	0.11
November	0.44	0.37	−0.17	−0.37	0.41	0.26	−0.41	−0.20	−0.06	−0.54	−0.62	−0.05
December	0.46	0.38	−0.13	−0.40	0.43	0.23	−0.44	−0.21	0.00	−0.55	−0.66	−0.06

Appendix. Continued

	Traits											
	<i>cw90</i>	<i>cw92</i>	<i>flr91</i>	<i>flr92</i>	<i>ht90</i>	<i>ht91_90</i>	<i>budbreak91</i>	<i>budbreak95</i>	<i>pests90</i>	<i>pests93</i>	<i>sd90</i>	<i>sd92</i>
Monthly precipitation												
January	-0.15	-0.07	0.03	0.18	-0.10	-0.26	0.16	0.25	0.31	-0.14	0.00	0.36
February	-0.18	-0.15	-0.02	0.14	-0.10	-0.28	0.13	0.28	0.35	-0.18	0.01	0.37
March	-0.18	-0.17	-0.07	0.15	-0.14	-0.25	0.10	0.29	0.38	-0.23	-0.05	0.33
April	-0.14	-0.17	-0.01	0.06	-0.04	-0.30	0.11	0.28	0.39	-0.22	-0.04	0.34
May	-0.15	-0.17	-0.03	0.00	0.00	-0.29	0.16	0.28	0.40	-0.16	-0.02	0.33
June	0.02	-0.01	0.12	-0.18	0.19	-0.23	0.13	0.10	0.25	-0.04	-0.01	0.31
July	0.16	0.18	0.10	-0.28	0.35	-0.12	-0.08	-0.12	0.03	-0.13	-0.15	0.15
August	0.19	0.24	-0.01	-0.25	0.38	-0.11	-0.04	-0.02	0.05	-0.31	-0.24	0.26
September	0.03	0.06	0.05	-0.11	0.23	-0.26	0.02	0.11	0.21	-0.23	-0.11	0.39
October	-0.08	0.02	0.00	0.06	0.02	-0.25	0.09	0.19	0.35	-0.25	-0.11	0.39
November	-0.22	-0.19	0.06	0.18	-0.15	-0.31	0.19	0.31	0.40	-0.14	0.07	0.35
December	-0.14	-0.08	0.02	0.18	-0.11	-0.29	0.16	0.28	0.31	-0.17	0.02	0.32

Significance levels are $r_{0.10} = 0.19$, $r_{0.05} = 0.31$, $r_{0.01} = 0.41$, $r_{0.001} = 0.51$, and $r_{0.0001} = 0.58$.

