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Thesis Title: Studies to Facilitate Reintroduction of Golden Paintbrush (*Castilleja levisecta*) to the Willamette Valley, Oregon.

THESIS CHAPTER 3

Common garden experiments with golden paintbrush (*Castilleja levisecta*): selecting seed sources and reintroduction sites for an endangered prairie species

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Chapter 3: Common garden experiments with golden paintbrush (*Castilleja levisecta*): selecting seed sources and reintroduction sites for an endangered prairie species

ABSTRACT

Species reintroduction is increasingly prescribed as a conservation strategy to promote the viability of endangered plants. A suite of ecological and genetic factors are likely to contribute to reintroduction success, including the ecological similarity between seed source and introduction site, the effective population size and genetic diversity of seed sources, and the habitat quality of the recovery site. We conducted common garden experiments with golden paintbrush (*Castilleja levisecta* Greenman), an endangered species endemic to the Pacific Northwest, U.S.A., and extinct in the southern portion of its historic range. We test hypotheses about how the species would perform in the southern portion of its range, as well as provide management recommendations about seed source and recovery site selection.

Ten common gardens, each comprised of *C. levisecta* individuals grown from seed collected from six of the eleven remaining source populations, were planted into field conditions similar to potential recovery sites in the Willamette Valley, OR, during two planting events in 2004. Significant variation among source populations and common gardens was observed for first year plant performance and second year survival rates. Plant community characteristics, including the abundance of non-native species and the similarity in community structure between source populations and common garden sites, helped explain the variation in these performance measures. Exotic species cover at common garden sites was associated with a reduction in performance of first year *C. levisecta* transplants. Survival of second year transplants increased with increasing similarity in plant functional groups between source and common garden sites, supporting the idea of a “home-habitat advantage.” These results indicate that high quality prairies, dominated by native perennial species with low non-native abundance, should be targeted for recovery sites. We do not recommend using genetic diversity, effective population size, or geographic distance to select seed sources for reintroduction of *C. levisecta* in the Willamette Valley. Instead, we recommend using plant material from Whidbey Island, WA, whose three populations represented in our study consistently performed well.

INTRODUCTION

Species reintroduction is a growing component of conservation efforts worldwide. Recovery plans recommended reintroduction or population augmentation to achieve recovery criteria for 87% of the federally listed plant species in 1997 (Kennedy 2004). However, despite numerous efforts, few, if any, reintroduction attempts can yet be judged as true successes (Bowles & McBride 1996; Bowles et al. 2001; Guerrant 1996b; Pavlik & Espeland 1998; Pavlik et al. 1993). Failure to achieve success is likely a result of our poorly developed biological understanding of species reintroduction (Falk et al. 1996). Selection of biologically appropriate seed sources and recovery sites is critical when implementing a reintroduction strategy, though few studies utilize both genetic and ecological criteria during the selection process (Husband & Campbell 2004). Decisions regarding the suitability of seed sources and recovery sites can be particularly challenging in portions of a species range that are currently uninhabited, as no reference populations with which to compare ecological and genetic characteristics exist. Currently, there are no published studies that have experimentally determined appropriate seed sources and/or recovery sites for plant reintroduction in an unoccupied portion of a species historic range. In order to evaluate relevant management options for reintroduction to the southern portion of the species' historic range, we conducted common garden experiments with golden paintbrush (*Castilleja levisecta*), an endangered plant endemic to the prairies of the Pacific Northwest.

The origin of source material used to establish new plant populations is a controversial issue in conservation biology. Habitat similarity between source and introduced populations may be crucial because of ecotypic differentiation and development of co-adapted gene complexes that form in response to specific habitat conditions and selective pressures (Guerrant 1996a; Guerrant & Pavlik 1998; Huenneke 1991; Hufford & Mazer 2003). Choosing an introduction site that closely matches the source site (i.e., soil, vegetation and climate) increases the likelihood that introduced plants will be genetically well-adapted to the site, and in turn, that introduction will succeed (Bowles et al. 1993; Montalvo & Ellstrand 2000; Pavlik et

al. 1993). Numerous studies have demonstrated a fitness advantage of local transplants relative to transplants from distant sites (Gustafson et al. 2004a; Montalvo & Ellstrand 2001; Schmidt & Levin 1985; Wang et al. 1997), emphasizing the importance of the home-site advantage, or what might be more broadly termed the “home-habitat advantage.” But how local is local (McKay et al. 2005)? Geographic distance is often used by land managers as an index of ecological similarity, because local sites are likely to share similar soils, vegetation, and climate. However, in a heterogeneous landscape and at great distances, geographic distance is not necessarily a good measure of ecological distance.

Characteristics of the seed source, such as population size and genetic diversity, could be powerful tools used to predict plant performance during plant restoration. Individuals from small populations are more susceptible to inbreeding depression, genetic drift, and the disruption of plant-pollinator interactions and are predicted to be less fit than those from large populations (Ellstrand & Elam 1993; Young et al. 1996). Population size and fitness components are positively related in several fragmented, rare vascular plants (Fisher & Matthies 1998; Menges 1991; Paschke et al. 2002). Similarly, population genetic theory predicts a positive correlation between genetic diversity and fitness (Young et al. 1996), and molecular marker diversity is therefore often used to decide which populations are most suitable as restoration sources (Haig 1998; Knapp & Rice 1998). However, this relationship may be weak, as genetic markers are generally considered neutral and genetic sampling is typically small relative to the size of the genome (Reed & Frankham 2003). No consistent pattern between marker diversity and plant performance emerges among rare, fragmented species. While some studies have found significant relationships (Buza et al. 2000; Oostermeijer et al. 1994; Paschke et al. 2002), others have not (Lammi et al. 1999; Luijten et al. 2000; Ouborg & Treuren 1995).

Exotic species constitute a significant component of many regional floras and are a major threat to global diversity (Hobbs & Humphries 1995). After habitat loss, non-native species are the most prevalent threat to endangered species viability, affecting half of the imperiled species in the U.S. (Wilcove & Master 2005). Pacific Northwest native grasslands are considered one of most critically endangered ecosystems in the nation

(Noss et al. 1995), with less than 3% of pre-settlement extent remaining (Chappell et al. 2000). Many of these remaining fragments are of poor quality due to isolation, fire suppression, and invasion by tall, aggressive pasture grasses that displace native flora. In turn, these grasses may enhance habitat for small mammals (Adler & Wilson 1989), whose abundance can influence grassland dynamics and species composition (Batzli & Pitelka 1970). Competition from non-native species has hindered reintroduction efforts of several rare species including *Abronia umbellata* (Kaye 2002), *Amsinckia grandiflora* (Pavlik et al. 1993), *Stephanomeria malheurensis* (Guerrant 1996b), and *Cirsium vinaceum* (Huenneke & Thomson 1995), suggesting that site quality and plant community characteristics are likely to play an important role in *C. levisecta* recovery as well.

Castilleja levisecta is a federally threatened species currently restricted to 11 sites in the Pacific Northwest and is extinct in the southern portion of its historic range. Recovery criteria call for the existence of twenty populations each composed of 1,000 flowering individuals within the species' historic range (U.S.F.W.S. 2000). *Castilleja levisecta* has limited capacity for natural dispersal and colonization of new sites, necessitating *ex situ* conservation techniques to meet recovery goals. A strategic reintroduction plan has been prepared to support the long-term viability of the species and requires establishment of new populations within the historic range of *C. levisecta*, including the Willamette Valley, Oregon (Caplow 2004).

Potential restoration sites in the Willamette Valley are geographically and ecologically distant from extant populations of *C. levisecta* (Chapter 2), with no indication of which seed source is most appropriate for recovery efforts in this ecoregion. Further, the specific habitat conditions to target during recovery efforts are unknown because the species has been extinct in this region for over 60 years and herbarium records do not clearly describe habitat characteristics (Chapter 2). Therefore, we apply ecological and genetic theory to restoration ecology in order to understand which factors could promote the reestablishment of *C. levisecta* in the Willamette Valley. Our main research objective is to determine what ecological and genetic factors contribute to the success of *C. levisecta* transplants in the southern portion of its historic range by testing three specific hypotheses. We will provide management recommendations based on these results.

Hypothesis 1: Performance of individuals decreases with ecological and/or geographic distance between source population and reintroduction site

Justification.- Selecting plant materials from sites that are ecologically similar to the introduction site may be most appropriate, as individuals from populations can be adapted to specific habitat conditions (Hufford & Mazer 2003). Local adaptation has been investigated using reciprocal transplant experiments in many studies (Cheplick 1988; Gordon & Rice 1998; Helenurm 1998; Kindell et al. 1996). However, no studies that we are aware of have attempted to extrapolate this concept to rare plant reintroduction in portions of the species' range that are no longer occupied. Geographic distance is often used by restoration practitioners as an index of ecological similarity, but it was not a good surrogate for environmental distance among populations of *Lotus scoparius* (Montalvo & Ellstrand 2000). According to Hypothesis 1, the success of reintroductions can be increased by targeting recovery sites that are ecologically similar and/or geographically close to the seed source.

Hypothesis 2: Plant performance is positively correlated with the size (N_e) and genetic diversity of the source population.

Justification.- Population genetic theory predicts that individuals from large, genetically diverse populations will be more fit than those from small, genetically depauperate populations (Young et al. 1996). Godt et al. (2005) observed a wide range of pairwise *C. levisecta* population genetic identities ($F_{st} = 0.055 - 0.388$), indicating that significant genetic differentiation among some remaining populations exists. Further, *C. levisecta* effective population size (N_e) and genetic diversity were generally positively correlated (Godt et al. 2005). Hypothesis 2 suggests that recovery efforts should use seed from large and genetically diverse populations.

Hypothesis 3: Transplant success is positively correlated with the habitat quality of the reintroduction site

Justification.- Biological characteristics of the reintroduction site, such as the presence of exotic species and generalist herbivores, can prevent effective plant recovery (Fiedler & Laven 1996). Extant populations of *C. levisecta* are threatened both by exotic

encroachment and herbivore pressure (U.S.F.W.S. 2000). Potential recovery sites in the Willamette Valley represent a continuum of habitat quality, ranging from abandoned agricultural fields dominated by exotic annuals to high quality prairies composed primarily of native perennial species. Many non-native species common to Pacific Northwest prairies are aggressive competitors and can displace native flora (Thomas & Carey 1996). Hypothesis 3 suggests that high quality sites dominated by native prairie plants with low herbivore abundance should be targeted for recovery efforts.

METHODS

Study species

Castilleja levisecta (Orobanchaceae) is a short-lived (5-6 years), multi-stemmed, perennial, endemic to the native grasslands of the Pacific Northwest. It is an out-crossing species primarily pollinated by *Bombus* spp. and is known only to reproduce by seed (Kaye & Lawrence 2003; Wentworth 2001). Like other members of the genus *Castilleja*, golden paintbrush is a facultative hemi-parasite (Kaye 2001b; Wentworth 2001). Although hemi-parasites are photosynthetic and do not require a host plant, they can form haustoria, or physical connections, with other root systems to obtain nutrients, water, and possibly secondary compounds from their host (Press 1989). *Castilleja levisecta* does not require a host to reproduce in a greenhouse environment and does not appear to be host specific (Wentworth 2001). Despite its rarity, a genetic analysis of *C. levisecta* indicates that the species maintains unusually high genetic diversity compared to other endemic species and even other members of the figwort family (Godt et al. 2005).

Ten of the eleven extant *C. levisecta* populations are concentrated in the San Juan Islands of Washington and British Columbia, generally on south-west facing coastal prairies with sandy, well drained soils of glacial origin (Chappell & Caplow 2004). Only one mainland population remains (Rocky Prairie), and is distinct from others because it is characterized by mounded topography (Chappell & Caplow 2004) and receives significantly more annual precipitation (129cm) than the island populations (52- 74 cm), which are located in the rain shadow of the Olympic Mountains (WRCC 2005). Despite relatively local distribution, extant populations are geographically fragmented and isolated from one another. Pollen flow may be limited

by the inability of pollinators to fly between island populations, the geographic isolation of Rocky Prairie, and the discontinuity of appropriate nectar sources in a landscape fragmented by agriculture and development (Godt et al. 2005).

Castilleja levisecta was last collected in the Willamette Valley in 1938 (Gamon 1995). The vegetation communities and soil characteristics of historic populations are not well understood because herbarium records do not specify exact locations or habitat characteristics of *C. levisecta* collections (Chapter 2). We believe the species inhabited upland prairies of the Willamette Valley, which are grass-dominated systems often associated with *Quercus garryana*-savanna, on well-drained soils commonly found on the valley foothills (Franklin & Dyrness 1988). The unglaciated soils of upland prairies are generally dominated by clay and silt from weathering basalt. Willamette Valley populations were likely subjected to a wetter climate (104 - 123 cm) than the majority of the extant populations in the Puget Trough (WRCC 2005).

Experimental design

Ten experimental common gardens were established throughout the species historic range in 2004. Nine common gardens were planted in the Willamette Valley, OR, the reintroduction target region. One common garden site was also established in the Puget Trough, WA near extant populations (Figure 3-1). Each common garden consisted of transplants from six source populations (Table 3-1), which were selected to characterize the geographic, genetic, and ecological diversity among the remaining eleven populations. Although we specifically selected sites with well-drained soils, the common garden sites encompassed a diversity of soil types, vegetation, and site quality, and are representative of locations likely to be chosen for future *C. levisecta* reintroduction endeavors (Chapter 2). Logistics also played an important role in site selection. Under the Endangered Species Act of 1973, listed plants are protected only on federal land. Therefore, seven of the ten potential recovery sites we chose to characterize were located on public land.

Table 0-1. Code, general location, habitat, and USGS soil map unit for each *C. levisecta* source population and common garden. (* denotes site without existing vegetation)

	code	general location	Habitat	Soil map unit
Puget Trough (extant populations)				
Ebey's landing	EBY	Whidbey Island, WA	coastal bluff	Rough broken land
Forbes Point	FRB	Whidbey Island, WA	coastal prairie	Coveland
Rocky Prairie	ROC	South Puget Trough, WA	mounded prairie	Spanaway-Nisqually
Trial Island	TRL	Trial Island, B.C.	coastal prairie	unavailable
West Beach	WEB	Whidbey Island, WA	coastal prairie	Bozarth
Kah Tai Prairie*	KAH	Port Townsend, WA	upland prairie	San Juan
Willamette Valley (reintroduction sites)				
Basket Butte 2	BB2	Baskett Slough National Wildlife Refuge, OR	upland prairie	Chehulpum
Basket Butte 3	BB3	Baskett Slough National Wildlife Refuge, OR	upland prairie	Chehulpum
Basket Slough 1	BS1	Baskett Slough National Wildlife Refuge, OR	upland prairie	Steiwer
Bell Fountain Prairie	BEL	Finley National Wildlife Refuge, OR	upland prairie	Jory
Heritage Seedling	HER	Salem, OR	restored prairie	Nekia
Pigeon Butte	PIG	Finley National Wildlife Refuge, OR	upland prairie	Dixonville
Plant Materials Center	PMC	Lewisburg, OR	agricultural field	Amity-Woodburn
Sandy River Delta	SRD	Troutdale, OR	degraded prairie	Burlington
Starck	STK	Dallas, OR	degraded prairie	Bellpine

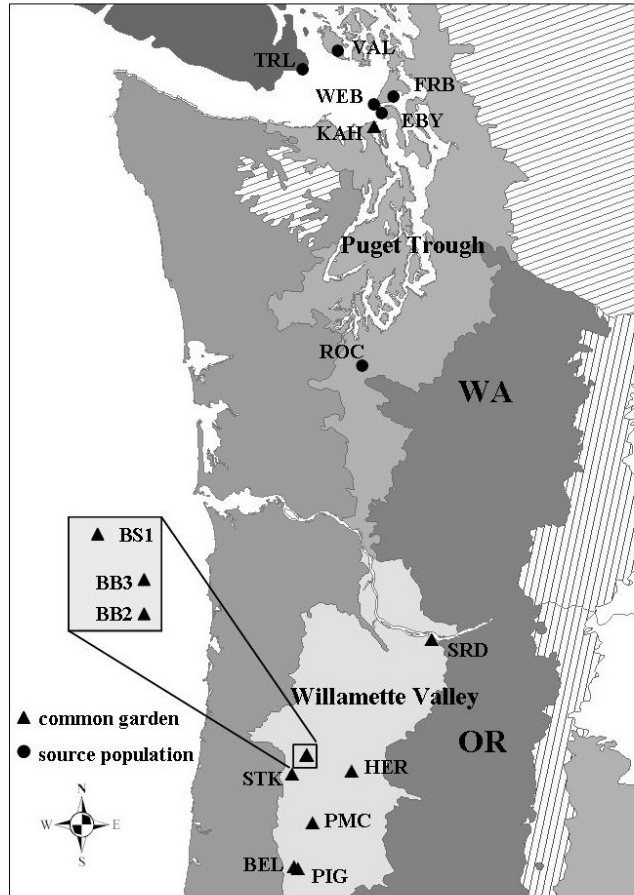


Figure 0-1. *Castilleja levisecta* source population and common garden sites located in the Pacific Northwest. Source populations and a single common garden site were situated in the Puget Trough, Washington. All other common gardens were located in the Willamette Valley, Oregon. For site abbreviations, see Table 3-1.

Common gardens were established in 2004 during two planting events. Seed was collected from 35 maternal plants from each source population in August 2003, and propagated according to Lawrence & Kaye (2005). Between 114 and 121 transplants were planted at each common garden site on March 1-5, 2004, for a total of 1168 spring transplants. Approximately 130 additional plants were planted at seven of the ten common gardens November 10-15, 2004, for a total of 905 fall transplants. Three common garden sites were not planted in fall 2004 because of poor spring 2004

transplant performance and a limited number of plants for the fall planting event. Variable germination and differential mortality during propagation prevented a genetically balanced design, though we attempted to equalize genetic representation of source populations and maternal lines at each common garden by planting an equal number of individuals from maternal lines at all sites. Three month-old transplants were randomized by source population and planting season and planted in the center of square meters within a 20m x 15m grid at each common garden site. Transplants were planted into sites with existing vegetation and were allowed to form haustorial connections with whatever root systems they encountered. However, the Plant Materials Center site was established in an agricultural field and individuals were provided with a grass host (*Festuca roemerii*). Two and a half meter fences were erected to enclose common gardens and protect transplants from deer and elk.

Measurement of plant size & survival

Castilleja levisecta individuals were monitored during peak prairie phenology in April-July, 2004 and 2005. Spring transplants were monitored three times during the 2004 growing season. Total stem length, number of stems, and flower and fruit production were recorded during each monitoring event. Vole activity was unusually high in the Willamette Valley during the 2005 growing season, when 89% of the surviving *C. levisecta* transplants were subjected to herbivory, most likely from grey-tailed voles (*Microtus canicaudus*). Continuous response variables such as stem length and number were not reliable measures of plant performance, as herbivory stimulated resprouting and altered plant morphology (B. Lawrence, pers. obs.). Therefore, we used survival as the response variable for 2005 analyses.

Community composition and soil variables

Species composition and abundance, as well as soil samples were collected during May 2004 at sites according to the methods outlined in Chapter 2. Soils were evaluated for physical (bulk density, percent sand, silt, and clay) and chemical (organic matter, pH, total organic carbon, total nitrogen, carbon to nitrogen ratio, nitrate, ammonium, potassium, phosphorus, manganese, magnesium, and sulfur) parameters. Access to the

San Juan Valley source population was restricted so no habitat information was collected there. This source population and the Plant Materials Center common garden site were not included in analyses requiring habitat information.

Statistical analyses

Transplant performance 2004

Because our measures of plant size and fitness (stem length, stem number, flower and fruit production) were correlated with one another, we combined them into a single index of plant performance using Principal Components Analysis (PCA) in PC-ORD v. 4.25 (McCune & Mefford 1999). The objective of PCA is to find the strongest linear correlation structure among variables and reduce them to a smaller number of synthetic variables that represent the most information in the original data set (McCune & Grace 2002). The maximum value of the three monitoring events for each parameter was used. Total stem length and stem number were log-transformed resulting in a normal, linear distribution of residuals. PCA scores from axis 1 were used as a measure of 2004 *C. levisecta* performance in further analyses.

Variation among sources and common gardens

We used analysis of variance (ANOVA) and binary logistic regression to test for effects of source population and common garden using S-PLUS v. 6.2 (Insightful 2000). ANOVA was used to compare mean plant performance of spring 2004 transplants (n= 1168). Binary logistic regression was used to analyze the variation in survival among source populations and common gardens for spring 2005 (n= 1168) and fall 2005 (n= 908) data. Significance was determined with drop in deviance tests using a chi-square distribution. Spring and fall transplants were analyzed separately for the 2005 analyses, as climatic variation and exposure to summer drought may have confounded observations from the two planting events. Pair-wise comparisons between source populations were corrected using Dunn-Sidak multiple comparisons.

Predictors of C. levisecta performance

In order to address our hypotheses, we developed seven predictor variables to determine if any helped explain the variation in *C. levisecta* performance and survival.

Ecological and geographic distance

To address Hypothesis 1, we developed measures of ecological and geographic distance between source populations and common gardens. We estimated ecological distance with two measures, soil distance and plant functional group distance.

Ecological distances were created using distance matrices in PC-ORD v. 4.25 (McCune & Mefford 1999). To estimate soil distance, or the dissimilarity of soil characteristics between sites, we used the mean value of each soil variable from all sites. Prior to calculation of a distance matrix, soil values were relativized by standard deviates that allow direct comparison of variables measured using different scales. Soil distance values were calculated using Euclidean distance because soil variables were generally linearly related.

We used plant functional groups to compare the similarity in plant community structure between sites because Puget Trough and Willamette Valley sites were floristically distinct (Chapter 2). Categorization of taxonomically diverse species into plant functional groups allows for evaluation of distinct plant communities that share ecological characteristics. Species were assigned to one of ten functional groups based on their origin (native vs. exotic), life history (annual vs. perennial), and habit (graminoid, forb, or woody). There were no annual woody species in our study system. Plant community distances were created with a Sorensen distance matrix, as recommended by McCune & Grace (2002), using the average cover value for each functional group from each site. Soil and community distances between each source population and common garden site combination were used as possible predictors of *C. levisecta* success in regression model selection.

Geographic distances between sites were calculated in Arcview 3.2 using the Bearing and Distance extension (ESRI 2000). All points were projected to Universal Transverse Mercator (UTM) with a Clarke 1866 ellipsoid and the North American Datum 1927 (NAD27). Preliminary screening of scatterplots suggested a weak, positive correlation between geographic distance and *C. levisecta* performance, which was

contradictory to the predicted relationship. Due to limited degrees of freedom and this unexpected relationship, we did not include geographic distance in the regression model building process. We report regression analyses of geographic distance and *C. levisecta* performance measures separately.

Source population size and genetic diversity

To address Hypothesis 2, we used estimates of source population size and genetic diversity as possible predictors of *C. levisecta* performance and survival. We used the observed heterozygosity of 13 allozyme markers from Godt et al. (2005) for each source population as estimates of genetic diversity. To estimate N_e for each source population, we utilized the harmonic mean of available census data between 1998 and 2003, which was log transformed to improve homoscedasticity. Census data were based on the number of flowering individuals from each population (F. Caplow unpublished data, Washington Natural Heritage Program).

Habitat quality of the reintroduction site

We used measures of common garden habitat quality, including exotic species abundance and herbivory rates, as possible predictors of *C. levisecta* performance and survival to address Hypothesis 3. Exotic species abundance was measured as the average cover of non-native plants at each common garden in 2004. Transplants planted in the spring of 2004 were subjected to various levels of herbivore pressure, including insect, small mammal, and possibly deer herbivory. Herbivory can have life-long impacts on the fitness of perennial species (Doak 1992). Therefore, we included the proportion of spring 2004 transplants subjected to herbivory in model selection for spring transplants.

Regression analyses

To test our hypotheses, we conducted separate regression analyses on spring 2004, spring 2005, and fall 2005 data sets. We used linear and binomial logistic regression to investigate the ability of predictors to account for variation in transplant performance and survival, respectively, using S-PLUS v. 6.2 (Insightful 2000). Mean 2004 transplant performance values (PCA scores) were used as the response variable ($n=$

45) in multiple linear regression analysis. Quasi-likelihood estimation was used to fit grouped binomial logistic regression models, using the proportion of 2004 transplants surviving to 2005 from each combination of source population and common garden as the response variable, for 2005 spring (n= 45) and fall (n= 30) transplants. Model selection for each data set was conducted using Bayesian Information Criteria (BIC), which evaluates the parsimony of models by comparing the reduction in the sum of squares with the addition of parameters to the model (Gotelli & Ellison 2004). Models with every one, two, and three predictor combinations, as well as null and full models were screened. Models with the lowest BIC value were interpreted. Predictors screened included: soil and community distance, source population N_e and observed heterozygosity, and common garden exotic plant cover and frequency of 2004 herbivory. Predictors not included in final models are not discussed in the results.

To test Hypothesis 1 with respect to geographic distance, we examined the relationship between geographic distance and spring 2004 performance (n= 45) using linear regression, and used grouped binomial logistic models for spring 2005 (n= 45), and fall 2005 (n= 30) survival.

Functional group patterns

We used Nonmetric Multidimensional Scaling (NMS) to investigate similarities in plant functional groups among source populations and common garden sites and develop recommendations for recovery site selection (Kruskal 1964; Mather 1976). The “slow and thorough” autopilot mode setting was used in PC-ORD v. 4.25 to ordinate sample units in functional group space (McCune & Mefford 1999).

RESULTS

Transplant performance 2004

Comparison of eigenvalues to those produced by a random model indicated that only axis 1 contained more information than expected by chance, supporting our decision to use scores from this axis in further analyses. Axis 1 accounted for 60.1% of the variance among performance measures and was strongly correlated with both stem length and number of stems, explaining 95.7% and 83.4% of their variation, respectively (Figure

3-2). Mortality during the first growing season was low. Thirty-three dead transplants, having values of zero for all four performance measures, are represented by the isolated point on the left end of axis 1. Table 3-2 shows the average performance measures associated with PCA scores for each source and common garden.

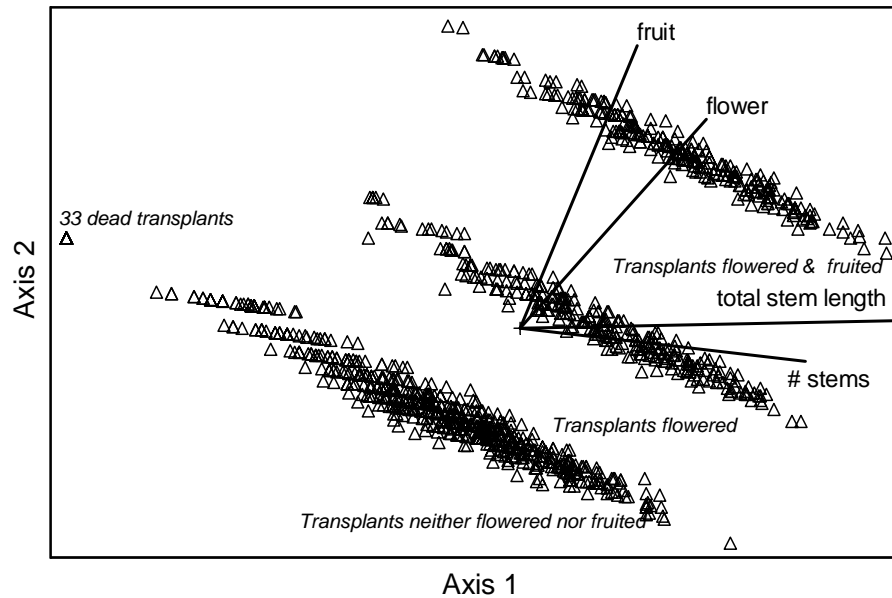


Figure 0-2. Plot of the first two principal components for 1168 *C. levisecta* transplants based on four performance variables. Each point represents a spring 2004 transplant. The solution was rotated to align the total stem length produced by transplants with axis 1. Vector overlays of the four variables were placed to depict the strength and direction of correlation with the two axes. The three bands represent different combinations of whether the transplant flowered and/or set fruit.

Table 0-2. Mean *C. levisecta* 2004 composite performance scores and field statistics for each source population and common garden (± 1 SE). Source populations not sharing a common letter were significantly different ($p \leq 0.05$) after Dunn-Sidak corrections.

	PCA score	stem length (cm)	# stems	% flowering	% fruiting
Source population					
Ebey's Landing ^{bc}	0.20 \pm 0.11	82.1 \pm 6.2	7.2 \pm 0.3	64.6 \pm 3.2	34.1 \pm 3.2
Forbes Point ^c	0.21 \pm 0.09	85.9 \pm 5.5	10.4 \pm 0.4	45.7 \pm 3.1	19.7 \pm 2.5
Rocky Prairie ^a	-0.75 \pm 0.16	47.5 \pm 6.1	6.9 \pm 0.5	20.5 \pm 4.5	12.0 \pm 3.6
Trial Island ^{bc}	-0.02 \pm 0.10	81.5 \pm 5.8	10.0 \pm 0.4	33.9 \pm 3.0	17.9 \pm 2.4
San Juan Valley ^{ab}	-0.38 \pm 0.12	57.0 \pm 6.2	8.4 \pm 0.5	37.3 \pm 4.0	11.3 \pm 2.6
West Beach ^{bc}	0.13 \pm 0.11	69.3 \pm 5.2	8.0 \pm 0.3	55.5 \pm 3.4	27.8 \pm 3.1
Common garden					
Basket Butte 2	-0.94 \pm 0.08	25.2 \pm 1.5	6.9 \pm 0.3	18.5 \pm 3.6	0 \pm 0
Basket Butte 3	0.46 \pm 0.12	65.0 \pm 5.8	10.3 \pm 0.6	19.3 \pm 3.7	0 \pm 0
Basket Slough 1	1.10 \pm 0.13	161.7 \pm 10.4	13.8 \pm 0.6	71.9 \pm 4.2	27.2 \pm 4.2
Bell Fountain	-0.38 \pm 0.15	53.2 \pm 4.3	5.1 \pm 0.3	44.7 \pm 4.7	28.1 \pm 4.2
Heritage Seedling	1.40 \pm 0.14	172.6 \pm 11.8	12.7 \pm 0.6	76.4 \pm 3.9	58.0 \pm 4.5
Kah Tai Prairie	-0.78 \pm 0.10	27.4 \pm 2.2	6.2 \pm 0.4	30.4 \pm 4.3	9.6 \pm 2.8
Pigeon Butte	0.29 \pm 0.11	89.5 \pm 6.8	8.8 \pm 0.5	60.0 \pm 4.5	15.0 \pm 3.3
Plant Mat. Center	1.2 \pm 0.11	89.3 \pm 5.4	7.9 \pm 0.4	89.7 \pm 2.8	75.0 \pm 4.0
Sandy River Delta	-0.53 \pm 0.10	33.8 \pm 2.6	8.9 \pm 0.4	30.2 \pm 4.3	6.0 \pm 2.2
Starck	-0.97 \pm 0.10	31.2 \pm 2.3	7.1 \pm 0.4	16.5 \pm 3.4	0.8 \pm 0.8

Variation among sources and common gardens

We observed differential performance among source populations ($F_{5, 1113} = 8.29$, $p < 0.001$) and common gardens ($F_{9, 1113} = 65.49$, $p < 0.001$) during the 2004 growing season (Table 3-2). Source populations performed similarly among common garden sites, as the interaction term between sources and common gardens was not significant ($F_{45, 1113} = 1.01$, $p = 0.45$). Transplants from the Trial Island source population, along with the three populations located on Whidbey Island, WA (i.e., Forbes Point, Ebey's Landing, and West Beach) were the top performers in 2004 (Table 3-2).

The mean proportion of spring transplants surviving to 2005 was 0.27 (SE = 0.013). Survival varied among spring 2005 transplants from different sources ($Dev_{5, 1113} = 33.25$, $p < 0.001$), and common gardens ($Dev_{9, 1113} = 327.55$, $p < 0.001$), but the interaction between these two main effects was not significant ($Dev_{45, 1113} = 52.12$, $p = 0.22$) (Table 3-3). Spring transplants from the Forbes Point and West Beach source populations (both located on Whidbey Island, WA) had significantly higher survival rates than Rocky Prairie, San Juan Valley, and Ebey's Landing in 2005, while Trial Island had

intermediate survival levels (Table 3-3). We observed little variation in fall transplant survival to 2005 which was generally high ($\bar{x} = 0.88$, SE= 0.011). Differential survival among common gardens ($Dev_{6, 866} = 54.35$, $p < 0.001$) was evident, but this was attributable to a single site (Pigeon Butte) that had significantly lower survival levels than all the other common gardens. Neither source populations ($Dev_{5, 866} = 2.27$, $p = 0.81$), nor the interaction term ($Dev_{30, 866} = 26.61$, $p = 0.64$) accounted for significant residual deviance.

Table 0-3. Average proportion of spring and fall transplants surviving in 2005 from each source population and common garden (± 1 SE). Source populations not sharing a common letter had significantly different ($p \leq 0.05$) 2005 survival rates as spring transplants after Dunn-Sidak corrections. Survival of fall transplants did not differ among sources.

	Spring 2005	Fall 2005
Source population		
Ebey's Landing ^a	0.22 ± 0.03	0.88 ± 0.03
Forbes Point ^b	0.32 ± 0.03	0.87 ± 0.02
Rocky Prairie ^a	0.16 ± 0.04	0.84 ± 0.04
Trial Island ^{ab}	0.28 ± 0.03	0.91 ± 0.02
San Juan Valley ^a	0.15 ± 0.03	0.87 ± 0.03
West Beach ^b	0.37 ± 0.03	0.87 ± 0.03
Common garden		
Basket Butte 2	0.22 ± 0.04	-
Basket Butte 3	0.05 ± 0.02	0.93 ± 0.02
Basket Slough 1	0.42 ± 0.05	0.91 ± 0.03
Bell Fountain	0.14 ± 0.03	0.88 ± 0.03
Heritage Seedling	0.24 ± 0.04	0.87 ± 0.02
Kah Tai Prairie	0.30 ± 0.04	0.97 ± 0.02
Pigeon Butte	0.51 ± 0.05	0.69 ± 0.04
Plant Materials Center	0.75 ± 0.04	0.95 ± 0.02
Sandy River Delta	0.04 ± 0.02	-
Starck	0.00 ± 0.00	-

Regression analyses

The abundance of exotic plants at common garden sites accounted for 20% of the variation in 2004 *C. levisecta* performance ($y = 0.93 - 0.018 * \text{exotic cover}$, $R^2 = 0.197$). Increasing exotic species cover was associated with decreased plant performance ($F_{1,46} = 10.56$, $p = 0.002$) (Figure 3-3).

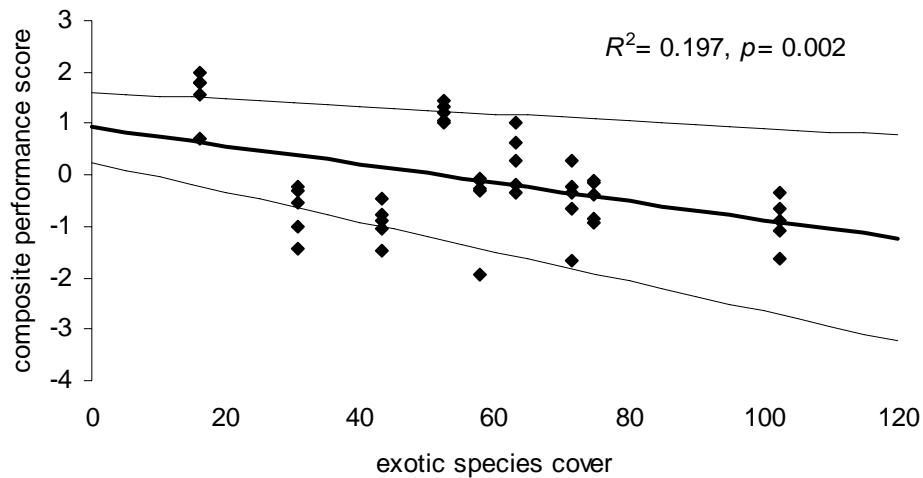


Figure 0-3. Scatterplot and fitted regression line of *C. levisecta* 2004 spring transplant composite performance as a function of exotic species cover at the common garden site. Dashed lines represent 95% confidence intervals.

The similarity of plant functional groups in plant communities between source populations and common gardens influenced the likelihood of *C. levisecta* spring transplant survival to 2005 ($Dev_{1,44} = 82.8, p < 0.001$). Plant community distance accounted for 35.3% of the residual deviance in survival of spring transplants. The probability of survival decreased as the similarity in plant functional groups between sources and common garden sites decreased (Figure 3-4). Survival rates of fall 2005 transplants varied little; model selection indicated that the null model was better than any of the other models screened.

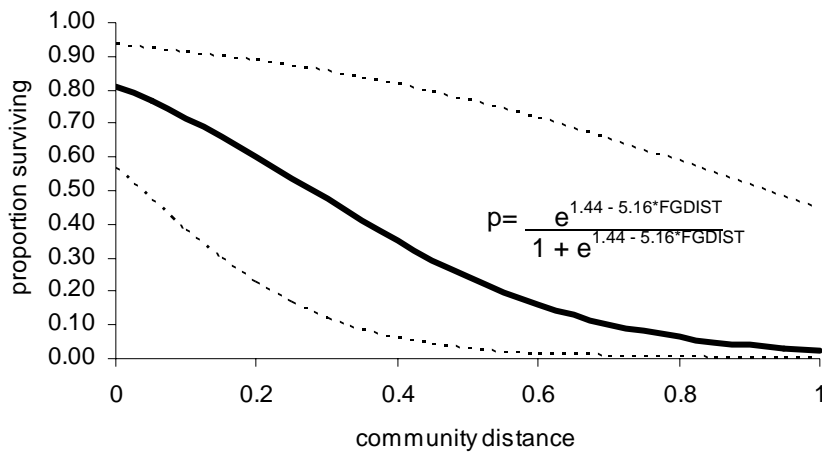


Figure 0-4. Survival of spring *C. levisecta* transplants to 2005 decreased with increasing community distance, which is a measure of the dissimilarity in plant functional group assemblage between source populations and common garden sites. Lower distance values represents greater similarity between sites. Dashed lines represent 95% confidence intervals accounting for overdispersion.

Plant performance in 2004 was weakly, but positively, correlated with the geographic distance between seed sources and common garden sites ($F_{43,1} = 4.86$, $R^2 = 0.10$, $p = 0.033$; Figure 3-5). Geographic distance was not a good predictor of spring ($DEV_{43,1} = 1.42$, $p = 0.232$) or fall transplant ($DEV_{28,1} = 3.21$, $p = 0.073$) survival.

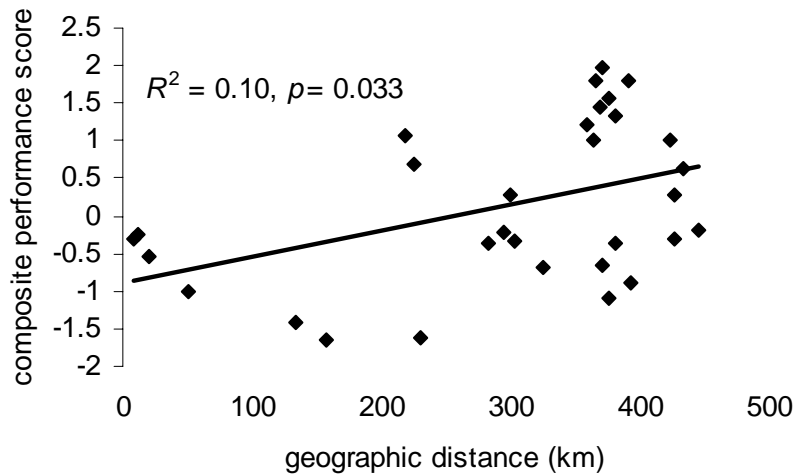


Figure 0-5. Scatterplot and trend line depicting a positive relationship between geographic distance and spring 2004 composite performance ($y = -0.96 + 0.003 * \text{geographic distance}$).

Functional group patterns

A 2-D solution explained 91% of the variation in the original data set. The final configuration had lower stress than those found with Monte Carlo randomizations ($p=0.020$). Most of the variation in plant functional groups was explained by axis 1 ($r^2=0.70$). The ordination was rotated to align the native perennial forbs group with axis 1, which had the strongest relationship with this axis ($r^2=0.73$).

Regional divergence in plant functional groups was evident among sites along axis 1 (Figure 2-3). Puget Trough sites aggregated on the right side of axis 1 which was strongly associated with native perennial forbs, grasses, and woody species ($r^2>0.35$). Exotic annual forbs and grasses were associated with the left side of axis 1 ($r^2>0.40$). In general, axis 1 represents a gradient from exotic annual to native perennial dominance. We observed low spring 2005 transplant survival at the common gardens Starck, Sandy River Delta, and Basket Butte 3, which were located on the left-hand side of the ordination space. Common garden sites on the right-side of axis 1, such as Pigeon Butte, Kah Tai Prairie, and Basket Butte 2, generally had a greater proportion of transplants surviving (Table 2-2). Axis 2 was strongly correlated with exotic perennials and native annual forbs ($r^2>0.45$).

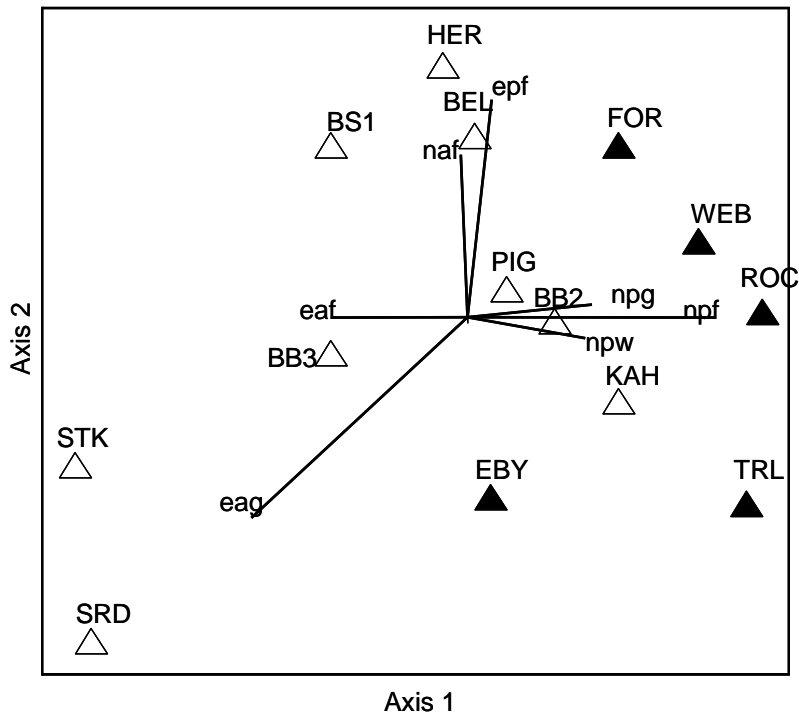


Figure 0-6. 2-D NMS solution of sample units in plant functional group space with functional group overlays. Each point represents a site (source population =▲, common garden sites=△). Vector overlays indicate the direction and strength of the relationship of plant functional groups with the axes. Axis 1 represents a gradient ranging from exotic annuals to native perennials. Vector labels are abbreviated: n= native, e= exotic, a= annual, p= perennial, g= graminoid, f= forb, w= woody. Abbreviations for source populations and common gardens are found in Table 3-1.

DISCUSSION

Ecological and geographic distance

Castilleja levisecta exhibits a “home-habitat advantage,” supporting a portion of Hypothesis 1 and suggesting that restoration sites ecologically similar to seed sources are more likely to have successful reintroductions than those that are ecologically distant. We observed higher second year transplant survival at common gardens with functional group assemblages similar to those of the transplant source population. Source populations were generally dominated by native perennial species; common gardens with similar assemblages had greater second year survival rates compared to those primarily composed of introduced annuals. Although geographic distance is often used as a measure of environmental similarity, it is not necessarily an appropriate index in this system, possibly because of the substantial differences in habitats and great distances

between extant and historic areas. Practitioners are often encouraged to use local genotypes during restoration activities, as local seed sources are more likely than non-local sources to experience similar selection pressures and be more genetically and ecologically appropriate for the recovery site (Gustafson et al. 2004b; Lesica & Allendorf 1999; McKay et al. 2005). We observed a weak, but significant, positive relationship between first year *C. levisecta* performance and the geographic distance between seed source and common garden site. This result is counter-intuitive to ecological theory and does not support the hypothesis that local sources are most appropriate for species recovery. This emphasizes the importance of using seed sources that are ecologically similar to the reintroduction site, regardless of the geographic distance involved. Matching environmental conditions between collection and restoration sites is likely to result in the use of ecologically appropriate genotypes and improve the likelihood of reintroduction success.

Source population N_e and genetic diversity

Conservation decisions are often based on population size and levels of genetic diversity without clear evidence of the correlation between these parameters and plant performance (Reed & Frankham 2003). We did not find support for Hypothesis 2, as neither effective population size nor observed heterozygosity were correlated with *C. levisecta* fitness. The two largest *C. levisecta* populations remaining, Rocky Prairie and San Juan Valley, consistently had the lowest germination, performance measures, and survival rates in our study. Our findings support the work of others that have found individuals from small populations to be as or more viable than larger populations (Lammi et al. 1999; Ouborg & Treuren 1995), emphasizing their potential value for *ex situ* conservation. Several studies suggest that the use of neutral markers is not an effective indicator of adaptive genetic differences (Britten 1996; David 1998; Savolainen & Hedrick 1995). Molecular markers reflect patterns of historical gene flow and genetic drift, but do not necessarily lead to a better understanding of a species' adaptive potential (McKay et al. 2005). Quantitative measures of phenotypic variation are considered to be better estimates of adaptively significant genetic diversity (Storfer 1996; Young et al. 1996), and are only weakly correlated with molecular marker diversity (Pfrender et al.

2000; Reed & Frankham 2001). Quantification of the genetic variation underlying traits associated with morphology, physiology, and life history attributes would likely be a more effective measure of adaptively significant variation in *C. levisecta*. Further examination of population dynamics of fragmented species is necessary to elucidate the mechanisms influencing plant performance with respect to population size and genetic diversity.

Habitat quality

We found strong evidence to support Hypothesis 3, as components of *C. levisecta* fitness were significantly influenced by the habitat quality of the reintroduction site. This is consistent with reviews of the avian and mammalian literature which indicate that translocation success is limited to sites with high quality habitat (Griffith et al. 1989; Wolf et al. 1996). *Castilleja levisecta* performance decreased with increasing abundance of non-native plants at common garden sites during the first growing season. Exotic species pose a serious threat to both remaining populations and reintroduction efforts, possibly because *C. levisecta* is a poor competitor or because non-native species are inappropriate hosts (further discussed below). While field herbivory during the first growing season did not significantly influence *C. levisecta* performance or second year survival, the 2005 population outbreak of the grey-tailed vole (*Microtus canicaudus*) impacted virtually all *C. levisecta* transplants in the Willamette Valley and devastated the grass seed crop in the region. Voles are important grassland herbivores subject to boom-bust cycles and are capable of altering vegetation dynamics in both native and agricultural systems. The 2005 outbreak was a regional phenomenon, as *C. levisecta* populations in Washington also suffered from vole herbivory (P. Dunwiddie, pers. comm.). A mild Pacific Northwest 2004-05 winter and the cyclical nature of vole abundance likely contributed to this occurrence.

C. levisecta competitive ability & host dynamics

The competitive ability of dominant species at recovery sites appears to be an important factor contributing to *C. levisecta* performance. *Castilleja levisecta* is a shade intolerant species, native to grasslands that were burned frequently by Native Americans

(Boyd 1986; Norton 1979). Fire suppression and exotic invasion has changed the community dynamics of remaining Pacific Northwest prairies (MacDougall et al. 2004). Invasion by exotic grasses coupled with abundant litter accumulation in these prairies may result in native species being outcompeted for abiotic resources. Exotic grasses may intercept light and limit the photosynthetic capacity of native competitors (D'Antonio & Vitousek 1992). Reproductive *C. levisecta* individuals reach an average height of 30 cm, while many exotic grasses common to the region are up to five times taller (e.g., *Arrhenatherum elatius*). *Castilleja levisecta* individuals growing beneath a canopy of grass and litter often appeared chlorotic and stressed. Other observations also indicate that *C. levisecta* may be a poor competitor. Transplant performance was greatest at three common garden sites that appeared to have low above-ground biomass, including the Plant Materials Center which had no above-ground biomass other than the *Festuca roemerii* host we provided. Two of these sites had been recently managed prior to common garden establishment; Heritage Seedling was tilled and seeded with native prairie species, while Basket Slough 1 had been burned. Habitat manipulations such as fire, herbicide application, and mowing are often employed to reduce competition from exotic species and can improve the growth and reproductive output of endangered plants (Guerrant 1996b; Kaye et al. 2001; Pavlik et al. 1993).

Native and appropriate host species may be limited at sites dominated by exotic annuals. Although *C. levisecta* is capable of utilizing a diversity of host species in the greenhouse, host quality and availability may be a limiting factor in the field. Fitness and survival of *C. levisecta* transplants was lowest at sites with a high abundance of exotic annuals, possibly because annuals allocate few resources to below-ground structures and die after reproduction. Host plants can provide water and nutrients to hemiparasites during periods of critical environmental stress (Press 1989). Systems dominated by annuals likely do not have sufficient below-ground resources to support *C. levisecta* individuals, especially during summer drought conditions typical of the Pacific Northwest, when annuals usually senesce. Perennial species are essential hosts for several other parasitic plants that live in arid habitats (Coats et al. 1993; Marvier & Smith 1997; Pate et al. 1990; Sprague 1962) and may allow parasites to take advantage of deep roots and enable them to exploit nutrients and water from a large volume of soil.

We have evidence that indicates co-planting a perennial host with *C. levisecta* transplants improves second year survival. The Plant Materials Center common garden was established in an agricultural field where *C. levisecta* transplants were planted with a perennial grass (*F. roemerii*). Spring transplant survival to 2005 was particularly high ($\bar{x} = 0.75$) at this site, and no *C. levisecta* individuals were observed without a live host. During experimental field studies with *C. levisecta*, Wayne (2004) found individuals co-planted with *F. roemerii* were more successful than those not provided with a host. Host plants were generally not provided in our study, allowing plants to make haustorial connections with existing root systems. Haustorial connections were evident between *C. levisecta* and nearby roots during excavation of some transplants, including *Arrhenatherum elatius*, a non-native perennial grass. Successful conservation and restoration of parasitic plants necessitates the management of thoughtfully selected host populations (Marvier & Smith 1997). We further investigated *C. levisecta* host requirements and preference in a companion study (Chapter 4).

Summer drought as a selective force

Summer drought appears to be a strong selective force resulting in differential transplant mortality. Natural populations of *C. levisecta* emerge in early March and become senescent in late summer in response to summer drought conditions (Caplow 2004). Survival was very high for first year transplants, and generally did not vary among sources or planting sites. At the time of monitoring in 2004, spring transplants had yet to experience a summer drought (nor had fall transplants when sampled in 2005). Survival rates for first year transplants were high (spring 2004 $\bar{x} = 0.99$, fall 2005 $\bar{x} = 0.88$), but dropped dramatically the second growing season (spring 2005 $\bar{x} = 0.22$). Others working with *C. levisecta* have also observed high second year mortality rates in the field (Swenerton 2003; Wayne 2004). Second year survival rates were greater for transplants that performed well during their first growing season compared with those that performed poorly (B. Lawrence, unpublished data), indicating that first year performance measures may be indicative of future survival.

Management Implications

Plant community composition of the reintroduction site will likely play a critical role in future *C. levisecta* recovery efforts. Our work suggests that high quality prairies should be targeted for reintroduction in the Willamette Valley, OR. Non-native plant cover at common garden sites was an important factor associated with reduced transplant vigor, suggesting that competitive interactions with exotic species are likely to play an important role in *C. levisecta*'s re-establishment. Native perennial communities are likely to support more host species that are appropriate for *C. levisecta* than those dominated by exotic annuals. Sites dominated by invasive species, particularly invasive annuals, should be avoided, while sites that are functionally similar to source populations, in particular those with high native perennial abundance, should be targeted. Although our results did not indicate that soil similarity influenced *C. levisecta* performance, we believe that sites in the Willamette Valley with relatively well drained soils are most appropriate since all remaining *C. levisecta* populations are found on well-drained sandy soils.

Active site management will be a critical component of *C. levisecta* reintroduction success. Steps to limit exotic abundance and the accumulation of biomass, as well as ameliorate native community composition and structure, should be taken at reintroduction sites. Clearly herbivore management, including voles as well as other mammals known to graze *C. levisecta* (i.e., deer, rabbits), will be an important component of recovery efforts and may coincide with habitat management objectives. Prescribed burns during times of *C. levisecta* dormancy have been used to manage vole populations at extant populations (P. Dunwiddie, pers. comm.). Fire consumes litter and reduces cover leaving voles more susceptible to predation and may also alleviate competition for light resources. Further, evidence suggests that *C. levisecta* responds favorably to fire in Washington prairies (Dunwiddie et al. 2000). Fencing may also be used to deter herbivores. Two and a half meter tall fences effectively excluded large mammals from our common garden experiments, and wire cages dug into the ground successfully prevented rabbit herbivory at a site on Whidbey Island (B. Lawrence, pers. obs.). A regional study aiming to promote native abundance in degraded Pacific Northwest prairies is currently investigating the effectiveness of management techniques that include burning, mowing, grass-specific herbicide use, and seeding with native

species. Results from this work will likely have relevant implications for prairie habitat management during *C. levisecta* recovery (T.N. Kaye, pers. comm.).

We do not recommend using genetic diversity, effective population size, or geographic distance as indices of appropriate *C. levisecta* seed sources for recovery efforts in the Willamette Valley. Instead we suggest that plant material from Whidbey Island populations be utilized, as these populations consistently had high germination rates, vigorous greenhouse growth, and superior field performance. Five of the eleven remaining populations of *C. levisecta* are found on Whidbey Island, three of which were represented in this study. Whidbey Island populations are relatively close together (within 15 km of each other), are considered to be ecologically similar (Chappell & Caplow 2004), and evidence suggests that recent gene flow has occurred among these populations (Godt et al. 2005). While the remaining *C. levisecta* populations on Whidbey Island are currently fragmented, these populations are considered a single genetic/geographical group and were probably less isolated from each other in the past (Chappell & Caplow 2004).

The merits of using single versus multiple seed sources during restoration activities is heavily debated in the conservation literature (Guerrant 1996a; Kaye 2001a). Recovery efforts utilizing plant material from a single source may restrict ecologically relevant genetic variation that is necessary for evolutionary resilience, and may also result in restored populations with cross-incompatible mating types (DeMauro 1993). Meanwhile, use of mixed seed sources can result in outbreeding depression, which is a growing concern in the restoration community (Hufford & Mazer 2003). We believe however that the use of multiple Whidbey Island sources for recovery efforts in the Willamette Valley is justified. We observed heterosis in the F1 during a preliminary analysis of *C. levisecta*'s breeding system, with increased size, flowering rate, and seed set with increasing genetic distance of the cross, ranging from self, sibling, intra-population to inter-population crosses (Kaye & Lawrence 2003). Based on these results, we would predict that reintroductions composed of genetic material from multiple source populations would have greater fitness and be more likely to succeed than those created from a single source, at least in the short term. Although outbreeding depression may not be detected until the F2 or further generations, this phenomenon is theoretically restricted to crosses between ecologically and genetically distinct populations. Currently, we

believe that the putative Whidbey Island meta-population is the most appropriate seed source for *C. levisecta* recovery efforts in the Willamette Valley, OR.

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