RESEARCH ARTICLE

Reintroduction of *Castilleja levisecta*: Effects of Ecological Similarity, Source Population Genetics, and Habitat Quality

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Abstract

A suite of ecological and genetic factors are likely to contribute to reintroduction performance. Potential factors include the ecological similarity between seed source and introduction site, population size and genetic diversity of seed sources, and the habitat quality of the introduction site. We conducted common garden experiments with golden paintbrush (*Castilleja levisecta*), an endangered species from the Pacific Northwest, U.S.A., in order to test hypotheses about reintroduction performance and to provide management recommendations. Ten common gardens, each composed of *C. levisecta* individuals grown from seed from six of the remaining populations, were planted into field conditions and monitored during two growing seasons. Plant community characteristics were important predictors of observed variation in *C. levisecta* performance.

Exotic species-cover at common garden sites was associated with a reduction in performance of first-year *C. levisecta* transplants, while survival to the second growing season increased with increasing similarity in plant functional groups between source and common garden sites. Although measures of genetic diversity, population size, and geographic distance are often used to make conservation decisions during species recovery, here they were poor predictors of *C. levisecta* performance and establishment. We recommend choosing material for reintroduction from ecologically similar habitats, rather than those most proximate geographically, and selecting recovery sites with low exotic species abundance.

Key words: common garden, ecological distance, endangered plant, geographic distance, habitat similarity, Pacific Northwest prairies, reintroduction.

Introduction

Species reintroduction is increasingly prescribed as a conservation strategy to promote the viability of endangered plants. For example, U.S. endangered species recovery plans recommended reintroduction or population augmentation to achieve recovery criteria for 87% of federally listed plant species in 1997 (Kennedy 2004). However, few reintroduction attempts have resulted in the establishment of viable populations (Pavlik et al. 1993; Guerrant 1996*b*; Bowles et al. 2001; Austin 2004; but see Maschinski & Duquesnel 2006). Failure to achieve success is likely a result of our poorly developed biological understanding of species reintroduction (Falk et al. 1996), and the myriad of ecological, genetic, and human-related factors that can affect reintroduction of endangered plants (Hogbin & Peakall 1999; Krauss et al. 2002; Menges 2008). 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 no longer inhabited, as no reference populations with which to compare ecological and genetic characteristics exist, and herbarium records rarely identify specific locations of historic populations. However, there are few 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 (but see Jusaitis et al. 2004).

Habitat similarity between source and reintroduction sites may be important because of ecotypic differentiation and development of coadapted gene complexes that form in response to specific habitat conditions and selective pressures (Hufford & Mazer 2003). Choosing a reintroduction site that matches the environmental characteristics of the source population increases the likelihood that introduced plants will be genetically well-adapted to the site, and in turn, that reintroduction will succeed (Pavlik et al. 1993; Montalvo & Ellstrand 2000). Numerous studies have demonstrated a

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fitness advantage of local transplants relative to transplants from distant sites (Montalvo & Ellstrand 2001; Gustafson et al. 2004*a*), emphasizing the importance of a home-site advantage, or what might be more broadly termed a home-habitat advantage. But how local is local (McKay et al. 2005)? Practitioners are often encouraged to use local genotypes during restoration activities, as nearby 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 (Lesica & Allendorf 1999; Gustafson et al. 2004*b*; McKay et al. 2005). However, in a heterogeneous landscape and at great distances, geographic proximity may not be a good measure of ecological distance.

Population size and genetic diversity are characteristics of the seed sources that are often used to predict plant performance during restoration. A recent meta-analysis found positive correlations between population size, fitness, and genetic variation; these relationships were especially strong in rare species (Leimu et al. 2006). Individuals from small populations are more susceptible to inbreeding depression, genetic drift, and the accumulation of deleterious mutations, and are predicted to be less fit than those from large populations (Ellstrand & Elam 1993; Young et al. 1996). Similarly, population genetic theory predicts a positive correlation between genetic diversity and fitness (Young et al. 1996), and molecular marker diversity is often used to decide which populations are most suitable as restoration sources (Haig 1998; Knapp & Rice 1998).

Exotic species constitute a significant component of many regional floras and are a major threat to global diversity. After habitat loss, non-native species are the most prevalent threat to endangered species viability, affecting half of the imperiled species in the United States (Wilcove & Master 2005), and hinder rare species reintroduction efforts globally (Pavlik et al. 1993; Huenneke & Thomson 1995; Walck et al. 1999; Jusaitis et al. 2004). Native prairies in the Pacific Northwest (U.S.A.) are considered a critically endangered ecosystem (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 restoration trajectories (Howe & Lane 2004).

Castilleja levisecta (golden paintbrush) is a threatened species currently restricted to 11 populations in the Pacific Northwest and is extinct in the southern portion of its historic range. *Castilleja levisecta* has limited capacity for natural dispersal and colonization of new sites, necessitating ex situ conservation to meet recovery goals (USFWS 2000). A reintroduction plan prepared to support the long-term viability of the species requires establishment of new populations within the species' historic range, including the Willamette Valley, Oregon (Caplow 2004). However, potential restoration sites in the Willamette Valley are geographically and ecologically distant from extant populations of *C. levisecta* (Lawrence

& Kaye 2006), with no indication of what seed sources or habitats to target during recovery efforts. The species has been extinct in the region for over 60 years and herbarium records do not clearly describe habitat characteristics (Gamon 1995; Lawrence & Kaye 2006).

We applied ecological and genetic theory to restoration ecology in order to understand which factors could promote the reestablishment of *C. levisecta* in nine common gardens planted in the Willamette Valley, Oregon. As recommended by Guerrant & Kaye (2007), we use an experimental framework to determine what ecological and genetic factors contribute to the success of *C. levisecta* outplantings in the southern portion of its historic range by testing a series of hypotheses: (1) Performance of individuals decreases with ecological and geographic distance between source population and reintroduction site, (2) plant performance is positively correlated with the effective population size and genetic diversity of the source population, and (3) establishment is positively correlated with the habitat quality of the reintroduction site.

Methods

Study Species

Castilleja levisecta (Orobanchaceae, formerly in Schrophulariaceae) is a short-lived (5–6 years) perennial, endemic to the grasslands of the Pacific Northwest. It is an out-crossing species primarily pollinated by *Bombus* spp. and is known only to reproduce by seed (Wentworth 2001; Kaye & Lawrence 2003). The species is a facultative hemi-parasite, but does not require a host to reproduce in the greenhouse and does not appear to be host specific (Kaye 2001*b*; Wentworth 2001).

Ten of the 11 extant *C. levisecta* populations are concentrated in the San Juan Islands of Washington (WA) and British Columbia (B.C.), 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), which receives more annual precipitation (129 cm) than island populations (52–74 cm; WRCC 2005), and is also the most geographically isolated and genetically divergent of the remaining populations (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 (Lawrence & Kaye 2006), but the species is believed to have inhabited upland prairies of the Willamette Valley. These prairies are grass-dominated systems often associated with *Quercus garryana*—savanna, on well-drained unglaciated soils commonly found on the valley foothills (Franklin & Dyrness 1988). Willamette Valley populations were likely subject 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. Nine common gardens were
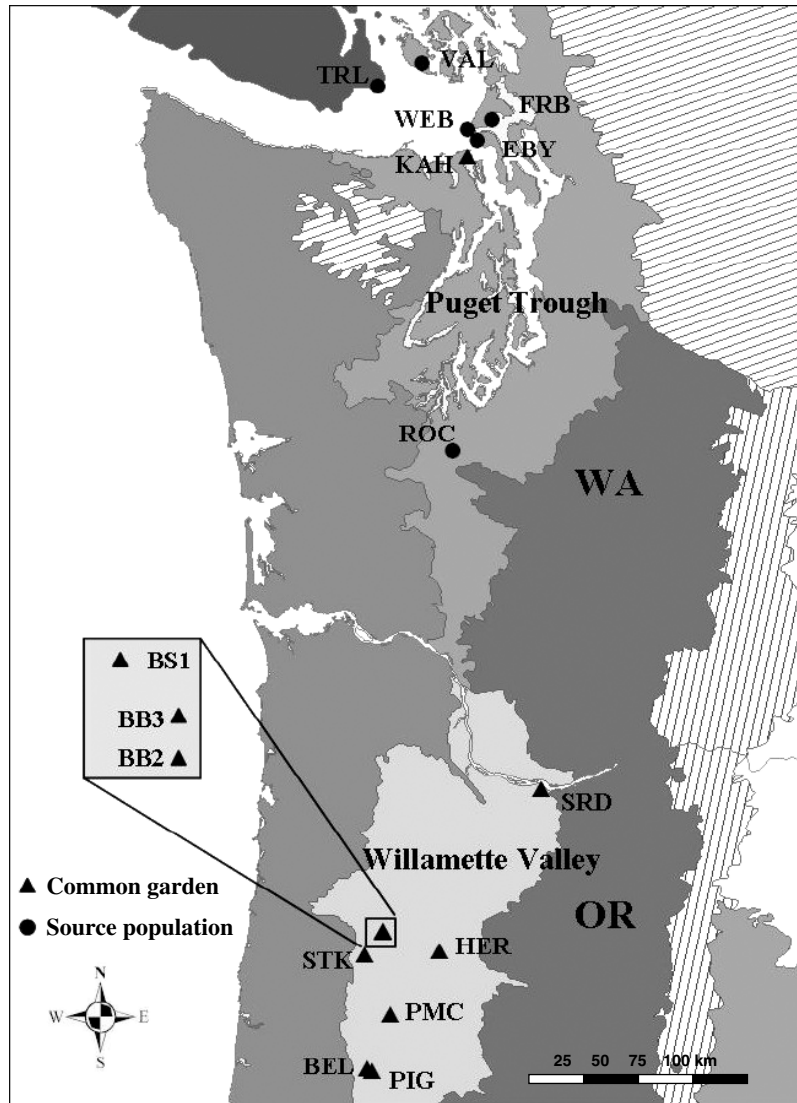
Figure 1. *Castilleja levisecta* source population and common garden sites located in the Pacific Northwest, U.S.A. Source populations and a single common garden site were situated in the Puget Trough, Washington. All other common gardens were located in the Willamette Valley, Oregon. For site abbreviations, see Table 1.

planted in the Willamette Valley, Oregon, the reintroduction target region. One common garden site was also established in the Puget Trough (WA) near extant populations (Fig. 1). Each common garden consisted of transplants from six source populations (Table 1). Although we specifically targeted sites with well-drained soils, the common garden sites encompassed a diversity of soils, vegetation, and site quality, and are representative of locations likely to be chosen for future *C. levisecta* reintroductions (Lawrence & Kaye 2006). Under the United States Endangered Species Act of 1973, listed plants are protected only on federal land. Therefore, we established 7 of the 10 potential recovery sites on federal property.

Common gardens were established in the week of March 1–5, 2004, within 20 × 15−m grids at each planting location. Seed was collected from 35 maternal plants from each source

population in August 2003, and propagated in a greenhouse according to Lawrence and Kaye (2005). Between 114 and 121 3-month-old plugs were planted at each common garden, for a total of 1,168 plants. We balanced genetic representation of source populations and maternal lines at each common garden by planting an equal number of individuals from each maternal line at all sites. Within each maternal line, individuals were randomly assigned a common garden site and position within the grid, and were planted in the center of a square meter grid cell. Transplants were planted into sites with existing vegetation and were allowed to form haustorial connections with encountered root systems. However, the Plant Materials Center site was established in an agricultural field, so individuals were provided with a native grass host (*Festuca roemeri*). Two and a half meter fences were erected

Table 1. General description of *C. levisecta* source population and common garden sites used in this study.

Sites	Code	Location	Habitat	Soil Texture
Puget Trough (extant populations)				
Ebey's Landing	EBY	Whidbey Island, WA	Coastal bluff	S
Forbes Point	FRB	Whidbey Island, WA	Coastal prairie	SCL
Rocky Prairie	ROC	South Puget Trough, WA	Mounded prairie	SL
Trial Island	TRL	Trial Island, B.C.	Coastal prairie	SL
West Beach	WEB	Whidbey Island, WA	Coastal prairie	SL
Kah Tai Prairie*	KAH	Port Townsend, WA	Upland prairie	SL
Willamette Valley (common garden sites)				
Basket Butte 2	BB2	Basket Slough NWR, OR	Upland prairie	SICL
Basket Butte 3	BB3	Basket Slough NWR, OR	Upland prairie	SICL
Basket Slough 1	BS1	Basket Slough NWR, OR	Upland prairie	SICL
Bell Fountain Prairie	BEL	Finley NWR, OR	Upland prairie	C
Heritage Seedling	HER	Salem, OR	Restored prairie	CL
Pigeon Butte	PIG	Finley NWR, OR	Upland prairie	C
Plant Materials Center	PMC	Lewisburg, OR	Agricultural field	SIC
Sandy River Delta	SRD	Troutdale, OR	Degraded prairie	SL
Starck	STK	Dallas, OR	Degraded prairie	SIC

NWR = National Wildlife Refuge; soil texture: C = clay; L = loam; S = sand; SI = silt. *Kah Tai Prairie is a common garden in the Puget Trough, not an extant population.

to enclose common gardens and protect transplants from ungulates.

Data Collection

Measurement of Plant Size and Survival. We monitored individuals three times during the 2004 growing season (May–July), and recorded total stem length, number of stems, and flower and fruit production. 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 gray-tailed voles (*Microtus canicaudus*). Continuous response variables such as stem length and number were not reliable measures of plant performance, because herbivory altered plant morphology and prevented flowering. Therefore, we used survival as the response variable for 2005 analyses. A companion host experiment revealed that survival of *C. levisecta* individuals planted without a host was minimally affected by vole activity (Lawrence & Kaye 2008).

Community Composition and Soil Characteristics. Species composition and abundance, as well as soil samples were collected during May 2004 at all sites using methods outlined in Lawrence and Kaye (2006). Soils were evaluated for physical (bulk density, soil texture) 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.

Predictors of *C. levisecta* Performance. We developed predictor variables to test our hypotheses and to examine the capacity of ecological similarity, characteristics of the

source population, and habitat quality of the introduction site to predict *C. levisecta* performance and survival.

Ecological Distance. Two measures of ecological distance based on the similarity between source population and common garden soil and plant functional group characteristics were developed. Ecological distances were created using distance matrices in PC-ORD v. 4.25 (McCune & Mefford 1999). Soil distances were calculated using Euclidean distance with the mean value of soil variables from each site (Lawrence & Kaye 2006). 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 (Lawrence & Kaye 2006). Species were assigned to one of nine functional groups based on their origin (native [n] versus exotic [e]), life history (annual [a] versus perennial [p]), and habit (graminoid [g], forb [f], or woody [w]): npg, naf, npf, npw, eag, eaf, epg, epf, or epw. Plant community distances were created using a Sorensen distance matrix with the average cover value for each functional group from each site (McCune & Grace 2002).

Geographic Distance. Geographic distances between sites were calculated in Arcview 3.2 using the Bearing and Distance extension (ESRI 2000). 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 selection process. We report regression analyses of geographic distance and *C. levisecta* performance measures separately.

Source Population Genetic Diversity and Size. Genetic analysis of extant *C. levisecta* populations was conducted by Godt et al. (2005). We used the observed heterozygosity (Ho) for each source population as an estimate of genetic diversity, as the observed and estimated heterozygosity of the

Table 2. Population size and observed heterozygosity (Ho) of the six *C. levisecta* source populations (Ho values from Godt et al. 2005).

Source Population	Population Size	Ho
Ebey's Landing	1,891	0.172
Forbes Point	1,282	0.258
Rocky Prairie	5,672	0.288
San Juan Valley	2,150	0.256
Trial Island	4,021	0.318
West Beach	299	0.203

13 allozyme markers they reported were strongly correlated ($r^2 = 0.97$), and other measures of genetic variation (i.e., P, allelic diversity) did not exhibit much variation. We used the harmonic mean of available census data between 1998 and 2002 to estimate population size because several populations had considerable variability in population size during this time period. Census data were based on the number of flowering individuals from each population (F. Caplow, unpublished data, Washington Natural Heritage Program). Observed heterozygosity and population size estimates for the six populations are listed in Table 2.

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. Exotic species abundance was measured as the average cover of non-native plants at each common garden in 2004. Herbivory can have life-long impacts on the fitness of perennial species (Doak 1992), so we included the proportion of transplants with evidence of herbivory in 2004 during model selection.

Statistical Analyses

Transplant Performance 2004. Because our measures of plant size and fitness (stem length, stem number, percent producing flowers and/or fruit) 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 maximum value of the three monitoring events was used because some plants were not observed at each monitoring event, due to plant phenology or sampling error. Total stem length and stem number were log-transformed to improve homoscedascity. PCA scores from axis 1 were used as a measure of 2004 *C. levisecta* performance in further analyses, as this axis accounted for 70.1% of the variance among performance measures.

Source Population and Common Garden Variation. We used analysis of variance (ANOVA) and binary logistic regression to test for effects of source population and common garden on 2004 performance and survival to 2005 ($n = 1,168$), respectively. Significance of binary logistic regressions was determined with drop in deviance tests using a chi-square distribution. The significance of all pair-wise comparisons was

assessed after Dunn-Sidak corrections using S-PLUS v. 6.2 (Insightful 2000).

Regression Analyses. To test our hypotheses, we conducted separate regression analyses on transplant performance in 2004 and survival to 2005. We used linear and binomial logistic regression to investigate the ability of predictors to account for variation in transplant performance and survival, respectively. Mean 2004 transplant performance values (PCA scores) were used as the response variable in multiple linear regression analysis. Quasi-likelihood estimation was used to fit grouped binomial logistic regression models, using the proportion of transplants surviving to 2005 from each combination of source population and common garden as the response. Individuals from the San Juan Valley source population and the Plant Materials Center common garden were not included in these analyses because habitat information was unavailable. Therefore, $n = 45$ (9 common gardens ×5 source populations) for each data set.

Model selection 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 (42 models total). Predictors screened included: soil and functional group distance, population size, observed heterozygosity, common garden exotic plant cover, and frequency of 2004 herbivory. Models with ΔBIC values < 2.0 were considered to have substantial support (Burnham & Anderson 2002), and those with the lowest BIC value were interpreted.

To investigate the relationship between geographic distance and *C. levisecta* performance, we used linear regression for the 2004 data set, and grouped binomial logistic models for transplant survival to 2005 ($n = 60$; 10 common gardens × 6 source populations).

Functional Group Nonmetric Multidimensional Scaling.

We used Nonmetric Multidimensional Scaling (NMS) to investigate similarities in plant functional groups among source populations and common garden sites to develop recommendations for recovery site selection (Kruskal 1964; Mather 1976). We ordinated sample units in functional group space using PC-ORD v. 4.25 (McCune & Mefford 1999).

Results

Source Population and Common Garden Variation

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 first growing season. Average performance measures associated with PCA scores for each source and common garden are presented in Table 3. Source populations performed similarly among common garden sites, as the interaction term between sources and common gardens was not significant ($F_{[45,1113]} = 1.01$, $p = 0.45$).

Table 3. Average *C. levisecta* 2004 PCA scores, associated growth parameters, and the average proportion of transplants surviving to 2005 for each source population and common garden site (±1 SE).

Sites	PCA Score	Total Stem Length (cm)	Number of Stems	Proportion Producing Flowers	Proportion Producing Fruit	Proportion Surviving to 2005
Source population						
Ebey's Landing*	0.20 ± 0.11^{bc}	82.1 ± 6.2	7.2 ± 0.3	0.65 ± 0.03	0.34 ± 0.03	0.22 ± 0.03^{a}
Forbes Point*	0.21 ± 0.09^{c}	85.9 ± 5.5	10.4 ± 0.4	0.46 ± 0.03	0.20 ± 0.03	0.32 ± 0.03^{b}
Rocky Prairie	-0.75 ± 0.16^{a}	47.5 ± 6.1	6.9 ± 0.5	0.21 ± 0.05	0.12 ± 0.04	0.16 ± 0.04^{a}
Trial Island	-0.02 ± 0.10^{bc}	81.5 ± 5.8	10.0 ± 0.4	0.34 ± 0.03	0.18 ± 0.02	0.28 ± 0.03^{ab}
San Juan Valley	-0.38 ± 0.12^{ab}	57.0 ± 6.2	8.4 ± 0.5	0.37 ± 0.04	0.11 ± 0.03	0.15 ± 0.03^{a}
West Beach*	0.13 ± 0.11^{bc}	69.3 ± 5.2	8.0 ± 0.3	0.55 ± 0.03	0.28 ± 0.03	0.37 ± 0.03^{b}
Common garden						
Basket Butte 2	-0.94 ± 0.08^{ab}	25.2 ± 1.5	6.9 ± 0.3	0.19 ± 0.04	0 ± 0	0.22 ± 0.04^{bc}
Basket Butte 3	0.46 ± 0.12^{cd}	65.0 ± 5.8	10.3 ± 0.6	0.19 ± 0.04	0 ± 0	0.05 ± 0.02^{a}
Basket Slough 1	1.10 ± 0.13^{e}	161.7 ± 10.4	13.8 ± 0.6	0.72 ± 0.04	0.27 ± 0.04	0.42 ± 0.05^{b}
Bell Fountain	-0.38 ± 0.15^{abc}	53.2 ± 4.3	5.1 ± 0.3	0.45 ± 0.05	0.28 ± 0.04	0.14 ± 0.03^{cde}
Heritage Seedling	1.40 ± 0.14^{e}	172.6 ± 11.8	12.7 ± 0.6	0.76 ± 0.04	0.58 ± 0.05	0.24 ± 0.04^{bcd}
Kah Tai Prairie	-0.78 ± 0.10^{a}	27.4 ± 2.2	6.2 ± 0.4	0.30 ± 0.04	0.10 ± 0.03	0.30 ± 0.04^{cd}
Pigeon Butte	0.29 ± 0.11^{d}	89.5 ± 6.8	8.8 ± 0.5	0.60 ± 0.05	0.15 ± 0.03	0.51 ± 0.05^{e}
Plant Mat. Center	1.2 ± 0.11^{e}	89.3 ± 5.4	7.9 ± 0.4	0.90 ± 0.03	0.75 ± 0.04	0.75 ± 0.04^{f}
Sandy River	-0.53 ± 0.10^{bc}	33.8 ± 2.6	8.9 ± 0.4	0.30 ± 0.04	0.06 ± 0.02	0.04 ± 0.02^{a}
Starck	-0.97 ± 0.10^{ab}	31.2 ± 2.3	7.1 ± 0.4	0.17 ± 3.4	0.01 ± 0.01	0.00 ± 0.00

Source populations or common gardens not sharing a common letter differed significantly ($p \leqslant 0.05$) after Dunn-Sidak corrections.
*Source populations located on Whidbey Island.

Transplants from the Trial Island source population, along with the three populations located on Whidbey Island, Washington (i.e., Forbes Point, Ebey's Landing, and West Beach) had the highest performance values during the first growing season (Table 3). The Heritage Seedling, Plant Materials Center, and Basket Slough 1 common gardens performed better than other reintroduction sites in 2004 (Table 3).

The mean proportion of transplants surviving to the second growing season was 0.27 (SE = 0.013). Survival to 2005 varied among 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). 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, whereas Trial Island had intermediate survival levels (Table 3). Individuals planted at the Plant Materials Center, an agricultural field, had the highest proportion surviving to 2005 (0.75). Other common gardens with relatively high survival included Pigeon Butte (0.51), Basket Slough 1 (0.42), and Kah Tai Prairie (0.30), all native, upland prairies.

Regression Analyses

Model selection revealed that variation in plant performance during the first growing season was best accounted for by exotic plant cover at the common garden site. The abundance of exotic plants at common garden sites accounted for 20% of the variation in *C. levisecta* performance ($y =$
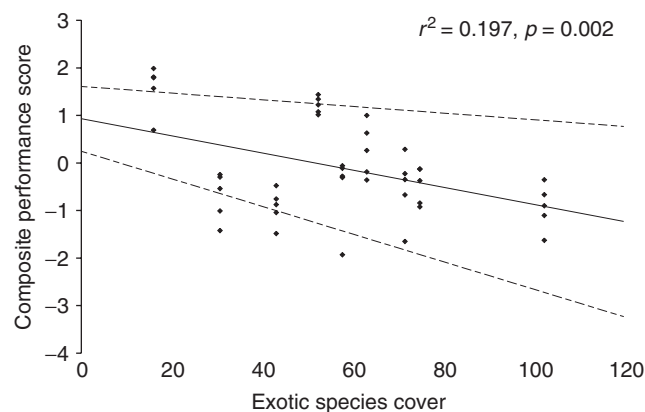

Figure 2. Scatterplot and fitted regression line of *C. levisecta* composite performance as a function of exotic species cover at common garden sites. Dashed lines represent 95% confidence intervals.

$0.93 - 0.018 \times$ exotic cover, $r^2 = 0.197$). Increasing exotic species cover was associated with decreased plant performance ($F_{[1,44]} = 10.56$, $p = 0.002$) (Fig. 2). Other models with low BIC scores included exotic cover and the ecological distance parameters as well as population size, but these models had ΔBIC values greater than two and were not further interpreted (Table 4).

The plant functional group distance parameter most appropriately modeled survival to the second growing season. Other models with low BIC scores included permutations with functional group distance, observed heterozygosity, and population size, as well as non-native cover (Table 5). The similarity of

Table 4. Models with the lowest BIC scores screened during model selection for 2004 *C. levisecta* performance.

Model	ΔBIC
Non-native	0
Non-native + FG distance + size	2.27
Non-native + FG distance	2.80
Non-native + size	3.12
Non-native + size + soil distance	3.43

FG = functional group; size = population size; Ho = observed heterozygosity.

Table 5. Models with the lowest BIC scores screened during model selection of *C. levisecta* survival to 2005.

Model	ΔBIC
FG distance	0
FG distance + Ho + size	2.81
FG distance + size	3.32
FG distance + Ho	3.45
Non-native	3.97

FG = functional group; size = population size; Ho = observed heterozygosity.

plant functional groups in plant communities between source populations and common gardens influenced the likelihood of *C. levisecta* 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. The probability of survival decreased as the similarity in plant functional groups between sources and common garden sites decreased (Fig. 3), supporting the idea of a home-habitat advantage.

Transplant performance in 2004 was weakly, but positively, correlated with increasing geographic distance between seed sources and common garden sites ($F_{[1,59]} = 7.77$, $r^2 = 0.12$, $p = 0.007$). However, this trend was strongly influenced by the poor performance of plants at the Kah Tai Prairie common garden located near extant populations, as well as the poor performance of plants grown from Rocky Prairie seed, the southern most source population. When these two groups were removed from the analysis, no relationship was observed ($F_{[1,44]} = 0.62$, $r^2 = 0.014$, $p = 0.434$).

Functional Group NMS

Regional divergence in plant functional groups was evident among sites along axis 1 of the NMS solution (Fig. 4), which was also the axis that explained most of the variation in plant functional groups ($r^2 = 0.70$). In general, axis 1 represented a gradient from exotic annual to native perennial dominance. 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 ($r^2 > 0.40$). We observed low second-year transplant survival at Starck, Sandy River Delta, and Basket Butte 3, which occupied the left-hand side of the ordination space. Common garden sites on the right side of axis 1, such as Pigeon Butte and Kah

Tai Prairie, generally had a greater proportion of transplants surviving to 2005 (Table 3). Axis 2 was strongly correlated with exotic perennials and native annual forbs ($r^2 > 0.45$), but explained little of the variation in plant functional groups ($r^2 = 0.30$).

Discussion

Ecological and Geographic Distance

Our findings support the conclusion that ecological distance, not geographic distance, is a useful measure for predicting plant establishment (Montalvo & Ellstrand 2000; Bischoff et al. 2006; Raabova et al. 2007). *Castilleja levisecta* exhibited a home-habitat advantage, suggesting that restoration sites that are ecologically similar to seed sources are more likely to support successful reintroductions than those that are ecologically distant. We observed higher second-year survival at common gardens with functional group assemblages similar to those of the source population. Source populations were generally dominated by native perennial species; common gardens with similar assemblages had greater second-year survival rates compared with those primarily composed of introduced annuals.

Although geographic distance is often used as a measure of environmental similarity, it is not an appropriate index in this system, possibly because of the substantial differences in habitats (Lawrence & Kaye 2006) and great geographic distances between extant and historic areas (~150–450 km). We observed higher first-year *C. levisecta* performance with greater geographic distance between seed source and common garden site, which does not support the hypothesis that local sources are most appropriate for species recovery. However, our study design had limited power to test the effect of geographic distance on reintroduced plant performance because only one common garden (Kah Tai Prairie) was established near source populations. Removal of the two sites with the smallest geographic distances (the northernmost common garden–Kah Tai Prairie, and the southern most source population–Rocky Prairie), eliminated the relationship between geographic distance and performance. Although it is unclear why *C. levisecta* transplants at Kah Tai performed relatively poorly in 2004, the poor performance of plants grown from Rocky Prairie seed may have a genetic basis. Rocky Prairie is geographically isolated and genetically distinct from other *C. levisecta* populations (Godt et al. 2005), which may result in selection for locally adapted genotypes that could reduce transplant performance away from their home site.

Our results suggest that it may be important to use seed sources that are ecologically similar to the reintroduction site (or vice versa), regardless of the geographic distance involved. Matching environmental conditions (i.e., plant community composition, soil characteristics, disturbance regimes) between collection and restoration sites is likely to result in the use of ecologically appropriate genotypes and improve the likelihood of reintroduction success.
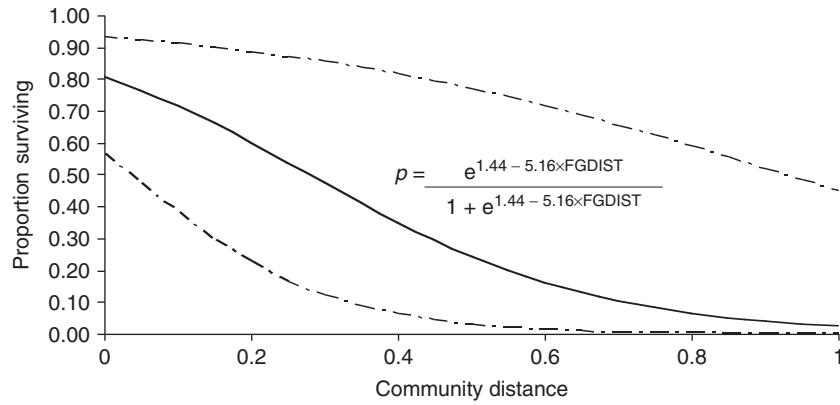
Figure 3. Survival of *C. levisecta* transplants to 2005 as a function of community distance (FGDIST), which is a measure of the dissimilarity in plant functional group assemblage between source populations and common garden sites. Lower distance values represent greater similarity between sites. Dashed lines represent 95% confidence intervals accounting for overdispersion.
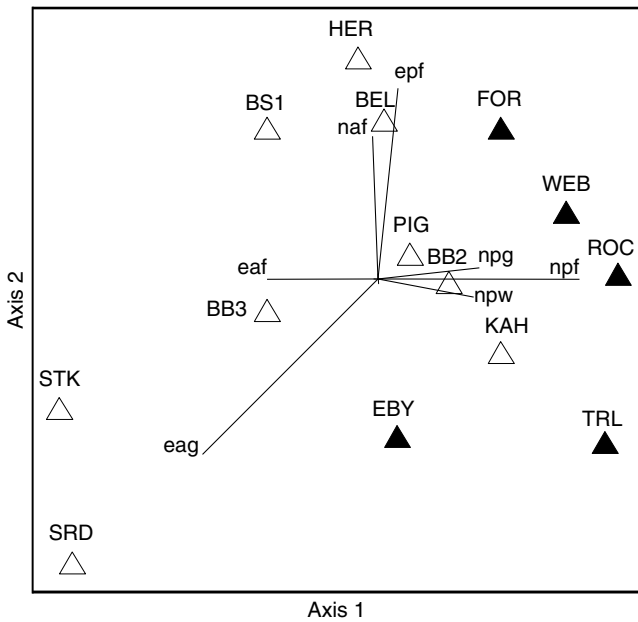

Figure 4. 2-D NMS solution of sample units in plant functional group space with functional group overlays. Each point represents a site (source population = ▲, common garden = △). Vector overlays indicate the direction and strength of the relationship of plant functional groups with the axes. Axis 1 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 1.

Source Population Size 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). Neither population size nor genetic diversity was strongly related to *C. levisecta* fitness, a pattern observed in many other plant systems (Ouborg & Treuren 1995; Lammi et al. 1999; Luijten et al. 2000; Peterson et

2008). 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 who have found that individuals from small populations can be as or more viable than larger populations (Ouborg & Treuren 1995; Lammi et al. 1999), emphasizing their potential value for ex situ conservation.

Despite its rarity, *C. levisecta* maintains unusually high genetic diversity ($H_{es} = 0.285$) compared with other endemic species ($H_{es} = 0.096$) and even other members of Schrophulariaceae ($H_{es} = 0.124$; Godt et al. 2005). However, allozymes, a neutral marker, may not be an effective indicator of adaptive genetic differences (McKay et al. 2005; Leimu et al. 2006), which may explain why we did not observe a relationship between heterozygosity and measures of *C. levisecta* fitness. 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*.

Habitat Quality

Consistent with the reviews of the avian and mammalian translocation literature (Griffith et al. 1989; Wolf et al. 1996), *C. levisecta* fitness was greatly influenced by the habitat quality of the reintroduction site. *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. Field observations suggest that *C. levisecta* is a poor competitor, intolerant of shade cast by tall exotic species and accumulated litter in fire suppressed prairies. Further, native perennial communities are likely to

support more host species that are appropriate for *C. levisecta* than those dominated by exotic annuals. Fitness and survival of *C. levisecta* transplants were lowest at sites with a high abundance of exotic annuals, possibly because annuals allocate few resources to belowground structures and die after reproduction. *Castilleja levisecta* may benefit from the attachment to perennial hosts during summer drought conditions typical of the Pacific Northwest (Pearson & Dunwiddie 2006).

Although field herbivory during the first growing season did not significantly influence *C. levisecta* performance or second-year survival, the 2005 population outbreak of the gray-tailed vole (*Microtus canicaudus*) was a regional phenomenon that influenced all *C. levisecta* common gardens and extant populations (P. Dunwiddie 2005, personal communication). Despite large populations in 2005, voles are ubiquitous in Pacific Northwest prairies and are major herbivores in grassland systems capable of altering species composition (Batzli & Pitelka 1970) and influencing restoration trajectories (Howe & Lane 2004). Effective recovery of *C. levisecta* will require herbivore control either through habitat manipulation or exclusion.

Seed Source Selection

The merits of using single versus multiple seed sources during restoration activities is heavily debated (Guerrant 1996*a*; Kaye 2001*a*; Hufford & Mazer 2003). Recovery efforts utilizing plant material from a single source or from just a few individuals may restrict ecologically relevant genetic variation that is necessary for evolutionary resilience (Krauss et al. 2002). Conversely, use of mixed seed sources can result in outbreeding depression (Becker et al. 2006), which is a growing concern in the restoration community (Hufford & Mazer 2003). Moving plant materials large distances to establish new populations also poses the risk of outbreeding depression through contact with resident populations. In this case, however, *C. levisecta* is locally extinct and concerns about interbreeding with remaining populations are unwarranted. We suggest that the use of multiple Whidbey Island sources for recovery efforts in the Willamette Valley may be justified because of the benefits of increased heterozygosity and the low risk of outbreeding depression. Heterosis occurs in *C. levisecta* in the F1 generation from between-population crosses as measured by plant size, flowering rate, and seed set (Kaye & Lawrence 2003). We predict that reintroductions composed of genetic material from multiple Whidbey Island sources will 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, we believe the risk of this occurring is low because Whidbey Island populations are ecologically and genetically similar (Chappell & Caplow 2004; Godt et al. 2005). On the basis of our common garden experiments, we believe that the Whidbey Island populations are the most appropriate seed source for initial *C. levisecta* recovery efforts in the Willamette Valley, Oregon.

Conclusions

Our study suggests that measures of ecological and geographic distance should not be used interchangeably during reintroduction of rare species, as geographic distance was a poor predictor of *C. levisecta* performance and survival. Source population size and observed heterozygosity were also not good predictors of *C. levisecta* fitness measures. Small, genetically depauperate populations of *C. levisecta* consistently performed well in our study, suggesting their potential importance for ex situ conservation. Our work contributes to the growing consensus that maximizing habitat similarity, specifically plant community characteristics, between source and introduction site increases the probability of plant establishment. Finally, our study highlights the importance of selecting high-quality reintroduction sites with minimal abundance of non-native species and that functionally resemble source populations.

Implications for Practice

- Choose recovery sites that share ecological characteristics (i.e., plant communities, soil characteristics) with the seed source. If sites do not share many species in common, target sites with similar dominant species or with similar functional groups.
- High-quality, native-dominated habitat should be targeted for rare plant reintroduction. Degraded sites with high abundance of exotic species should be avoided or may need to be restored prior to introducing rare species.
- Potential herbivores should be identified prior to rare plant introduction and steps to reduce herbivore levels at recovery sites should be implemented (e.g., habitat manipulation, fencing, etc.).
- Common garden experiments can be an effective way to identify appropriate seed sources and recovery sites prior to large-scale reintroduction of endangered plants.

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