Beth A. Lawrence, Oregon State University, Department of Botany and Plant Pathology, Corvallis, Oregon 97330

and

Thomas N. Kaye[1], Institute for Applied Ecology, 563 SW Jefferson, Corvallis, Oregon 97333

Habitat Variation Throughout the Historic Range of Golden Paintbrush, a Pacific Northwest Prairie Endemic: Implications for Reintroduction

Abstract

Although golden paintbrush historically inhabited the prairies of the Willamette Valley, Oregon, this Pacific Northwest prairie endemic is currently restricted to eleven sites in the Puget Trough of Washington and British Columbia. Recovery criteria call for the establishment of new populations throughout the species' historic range, including the Willamette Valley. We described vegetation and soil characteristics of representative golden paintbrush recovery sites in the Willamette Valley and compared them with those of remaining golden paintbrush populations in the Puget Trough. Potential golden paintbrush habitat in the Willamette Valley was ecologically distant from remaining populations. This disparity was likely related to regional differences in geology, climate, ocean proximity, and land-use history. Many of the species indicative of remaining populations in the Puget Trough were native perennials, while those of potential reintroduction sites in the Willamette Valley were introduced annuals. Soil characteristics of golden paintbrush sites were also distinct among the two ecoregions. Puget Trough sites were located on sandy soils with generally high levels of magnesium and sulfur, while Willamette Valley sites were found on silty-clay soils with high concentrations of potassium and phosphorous. Differences in soil texture, and magnesium and potassium concentrations were associated with plant community divergence among the two regions. We suggest using a plant functional group approach when comparing vegetation assemblages among Puget Trough and Willamette Valley sites, which allows comparison of taxonomically distinct communities that share ecological characteristics.

Introduction

As defined by The World Conservation Union, reintroduction is "an attempt to establish a species in an area which was once part of its historical range, but from which it has been extirpated or become extinct" (IUCN 1998). Successful plant reintroduction requires evaluation of the species' physical and biological habitat (Fiedler and Laven 1996) because selection of appropriate seed sources and recovery sites is crucial when implementing a recovery strategy (McKay et al. 2005). Habitat similarity among seed sources and prospective planting sites is important because populations may be adapted to specific habitat conditions and selective pressures (Huenneke 1991, Guerrant 1996, Guerrant and Pavlik 1998, Hufford and 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, Pavlik et al. 1993, Montalvo and Ellstrand 2000).

Decisions regarding the suitability of seed sources and recovery sites can be particularly challenging in portions of a species former range that are no longer inhabited, as no reference populations exist with which to compare ecological and genetic characteristics. Further, substantial changes in ecosystem function, including habitat loss, invasion, and alterations to the disturbance regime, will likely have occurred since the species was last observed (MacDougall et al. 2004). Golden paintbrush (*Castilleja levisecta*; Orobanchaceae) is a federally listed endangered plant endemic to the prairies of the Pacific Northwest and is currently extinct in the southern portion of its historic range, which includes the Willamette Valley, Oregon. Reintroduction of *C. levisecta* to this ecoregion is a priority for its recovery (U.S.F.W.S. 2000, Caplow 2004). However, *C. levisecta* has not been observed in the Willamette Valley since 1938 and there is limited information about the location and site characteristics of historic populations (Gamon 1995).

Although there are herbarium specimens from six possible historic *C. levisecta* populations in the Willamette Valley, OR, the vegetation and soil characteristics of these populations are not well

[1]Author to whom correspondence should be addressed. Email: kayet@peak.org

© 2006 by the Northwest Scientific Association. All rights reserved.

understood. Herbarium records generally do not specify the exact location or habitat characteristics of extirpated populations. Further, much of the potential habitat in the vicinity of historic locales has been converted to agricultural use or developed commercially. Below are brief descriptions of Willamette Valley collections as outlined by Gamon (1995). *Castilleja levisecta* was first collected in Oregon in 1905 in Bonneville, Multnomah County by an unidentified collector. Potential habitat in this area was likely destroyed with construction of the Bonneville Dam beginning in 1937. There are three collections from Marion County, OR; Peck collected *C. levisecta* in 1910 from "damp open ground, Salem," and J.C. Nelson made two 1916 collections and labeled specimens as "wet meadow, Salem," and "wet meadow, 3 miles south of Salem." There are four *C. levisecta* collections from Linn County, OR. A 1922 specimen from an unknown collector simply states the location as "Brownsville." Similarly, there is also a geographically vague 1929 collection from "Lebanon, OR." There are two *C. levisecta* collections from Peterson Butte in 1938; E.M. Harvey collected *C. levisecta* in a prairie along a stream at the south west base of Peterson's Butte, and Whitaker collected the plant at "Peterson Butte Cemetery." We recently visited Sand Ridge Cemetery which is located on the south west flank of Peterson's Butte and observed gravelly soils that appeared to be well-drained and several prairie species including *Camassia quamash*, *Dodecatheon hendersonii*, *Fritillaria affinis*, and *Danthonia californica*. It is possible that Sand Ridge Cemetery is the same site as Whitakers's "Peterson Butte Cemetery."

Based on these records and our observations, it appears that *C. levisecta* inhabited the once abundant grasslands of the Willamette Valley that were maintained by fire initiated by Native Americans (Boyd 1986). The collection sites for several of the specimens are described as damp or moist, but it is not clear whether these populations occurred in wetland prairies with poor drainage, or in upland prairies associated with well-drained soils, as collections were generally made in spring (i.e., May) when soils were likely still saturated. The probable locations of the "Bonneville" and "3 miles south of Salem" collections suggest that *C. levisecta* was potentially associated with gravel outwashes of the Columbia and Santiam Rivers, respectively. We believe that *C. levisecta* historically inhabited upland prairies in the Willamette Valley, because all of the remaining populations in the Puget Trough are associated with sandy, well-drained soils of glacial origin (Chappell and Caplow 2004). In general, potential recovery sites in the Willamette Valley are grass-dominated systems associated with *Quercus garryana*-savanna, commonly found on the valley foothills (Franklin and Dyrness 1988). The unglaciated soils of Willamette Valley upland prairies are typically composed of clay and silt from weathering basalt and are considered to be well-drained.

Here, we describe the variation in habitat characteristics among potential recovery sites in the Willamette Valley, OR and several extant *C. levisecta* populations located in the Puget Trough ecoregion. We examine plant communities and soil characteristics of experimental *C. levisecta* reintroduction sites and source populations used in a common garden study that was initiated to facilitate management decisions regarding seed selection and recovery site criteria in the southern portion of the species' range (Lawrence 2005). Our objective is to describe patterns of habitat differentiation among *C. levisecta* source populations and potential reintroduction sites in the Willamette Valley, as well as to explore the management implications of range-wide habitat variation for recovery efforts.

Methods

Study Sites

Five extant *C. levisecta* populations in the Puget Trough were included for comparison to nine sites in the unoccupied, historic range in the Willamette Valley (Table 1, Figure 1). One additional experimental site (Kah Tai Prairie) near Port Townsend, WA was also included because of its proximity to remaining populations on Whidbey Island. The ten experimental sites were the locations of common gardens established in 2004 and encompassed a diversity of soils, vegetation, and site quality, and are representative of sites likely to be chosen for future *C. levisecta* reintroduction (Lawrence 2005). The experimental locations were not the sites of known historic populations, as specific geographic locations of historic populations are either unknown or are located on private property. We specifically targeted sites in the Willamette Valley with well-drained soils because remaining *C. levisecta* populations in the Puget Trough are found on sandy soils. Logistics also played an

TABLE 1. Code, eco-region, site type, general location, habitat type, and USGS soil series mapping unit for each *Castilleja levisecta* site.

C. levisecta Site	Code	Eco-region	Site Type	General Location	Habitat	Soil Map Unit
Ebey's Landing	EBY	Puget Trough	extant	Whidbey Island, WA	coastal bluff	Rough broken land
Forbes Point	FRB	Puget Trough	extant	Whidbey Island, WA	coastal prairie	Coveland
Rocky Prairie	ROC	Puget Trough	extant	South Puget Trough, WA	mounded prairie	Spanaway-Nisqually
Trial Island	TRL	Puget Trough	extant	Trial Island, B.C.	coastal prairie	unavailable
West Beach	WEB	Puget Trough	extant	Whidbey Island, WA	coastal prairie	Bozarth
Kah Tai Prairie	KAH	Puget Trough	reintro	Port Townsend, WA	upland prairie	San Juan
Basket Butte 2	BB2	Willamette Valley	reintro	Baskett Slough NWR, OR	upland prairie	Chehulpum
Basket Butte 3	BB3	Willamette Valley	reintro	Baskett Slough NWR, OR	upland prairie	Chehulpum
Basket Slough 1	BS1	Willamette Valley	reintro	Baskett Slough NWR, OR	upland prairie	Steiwer
Bell Fountain Prairie	BEL	Willamette Valley	reintro	Finley NWR, OR	upland prairie	Jory
Heritage Seedling	HER	Willamette Valley	reintro	Salem, OR	restored prairie	Nekia
Pigeon Butte	PIG	Willamette Valley	reintro	Finley NWR, OR	upland prairie	Dixonville
Plant Materials Center	PMC	Willamette Valley	reintro	Lewisburg, OR	agricultural field	Amity-Woodburn
Sandy River Delta	SRD	Willamette Valley	reintro	Troutdale, OR	degraded prairie	Burlington
Starck	STK	Willamette Valley	reintro	Dallas, OR	degraded prairie	Bellpine

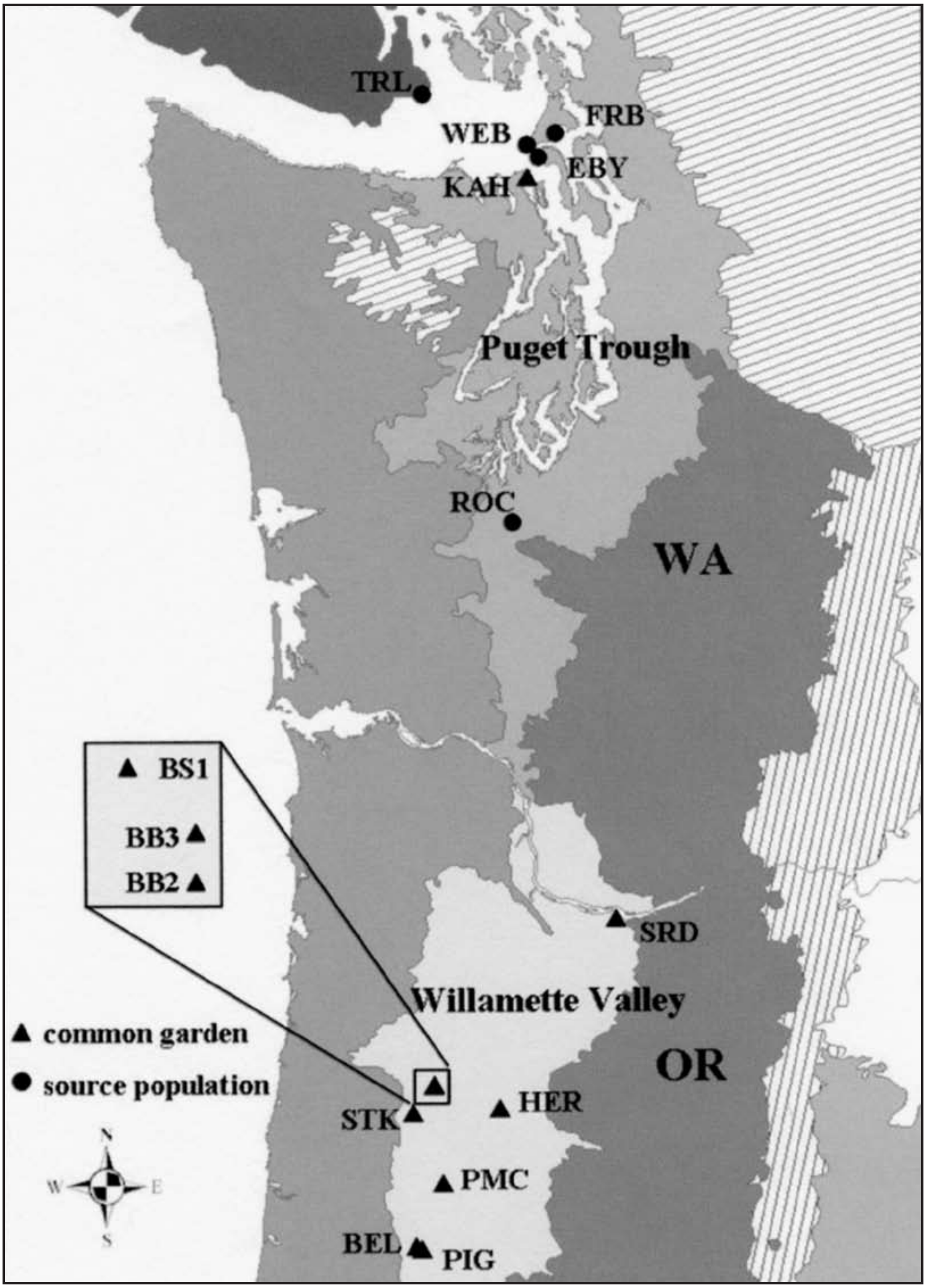

Figure 1. *Castilleja levisecta* extant populations and reintroduction sites located in the Pacific Northwest. Source populations and one reintroduction site are situated in the Puget Trough, Washington. The nine other reintroduction sites are located in the Willamette Valley, Oregon. See Table 1 for site abbreviations.

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 characterized were located on federal land.

Vegetation Sampling

Plant community composition data were collected at all sites in May 2004, when phenology was optimal for observing most graminoid and forb species. Visual estimates of percentage cover were made for each vascular plant species present within three randomly placed 5 x 5 m plots at each reintroduction site. One of the reintroduction sites (Plant Materials Center) was established in a cleared agricultural field with no vegetative cover and was not included in vegetation analyses. For extant populations, we used community data collected by C. Chappell (Washington Department of Natural Resources), who placed 5 x 5 m plots in dense areas of *C. levisecta* and recorded percentage cover values of all species. Number of plots within extant populations varied among sites (n = 1 to 4), depending on the number of distinct plant communities at each site (see Chappell & Caplow 2004). We assisted C. Chappell with data collection at three of the extant populations to calibrate estimates of species cover. Over all, we utilized data collected from 38 plots among 14 sites (5 extant, 9 experimental) to describe the variation in plant communities at current *C. levisecta* populations and potential reintroduction sites. Species nomenclature from the USDA PLANTS database was used (USDA-NRCS 2006).

Soil Sampling and Characterization

We collected soil samples from each site, except the source population Trial Island, in May 2004 using an impact soil corer of known volume to 15 cm depth. Ten random samples were taken at each site and thoroughly mixed. Soil was collected from Trial Island, B.C., on 21 April 2004 by M. Fairbarns of Aruncus Consulting, who took two samples from each of four sampling sites following the methods of Chappell & Caplow (2004), and sent them to us at Oregon State University. We evaluated soils 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) properties. The bulk density (D_b) of each sample was calculated as the oven-dry mass (g) of the composite sample divided by its volume (cm^3). Trial Island soils were not evaluated for bulk density because an unknown volume of soil was collected. Two sub-samples of the bulked soil from each site were analyzed for each of the other soil properties measured. Soil texture (% sand, silt, and clay) was calculated using the hydrometer method. The loss on ignition method was used to determine the percent organic matter content (% OM). We used a Lachat QuickChem 4200 analyzer with QuickChem 10-107-06-2-A NH4 and 10-107-04-1-A NO3 to measure ammonium (NH_4) and nitrate (NO_3), and Shimadzu TOC-V and Shimadzu TNM-1 to measure total organic carbon (TOC) and total nitrogen (TN). The carbon to nitrogen ratio (C:N) was calculated by dividing the mean total organic carbon by the mean total nitrogen for each site. All other elemental analyses were conducted using an ICP OES-Optima 4300 DV.

Regional Patterns in Habitat Characteristics

To identify differences among plant communities throughout the historic range of *C. levisecta*, we used Indicator Species Analysis to assign an indicator value to each species by combining the relative abundance and frequency of species from two predefined groups, Puget Trough and Willamette Valley (Dufrene and Legendre 1997, McCune and Grace 2002), using PC-ORD v. 4.25 (McCune and Mefford 1999). Indicator values range from zero (no indication) to 100 (perfect indication). We present the absolute mean cover values for the 15 species with the highest indicator value from each site in the Puget Trough and Willamette Valley ecoregions. To examine floristic similarities between the two regions, we present average cover values for species that occur at no less than half of the 14 sites.

We used Nonmetric Multidimensional Scaling (NMS) to investigate patterns of habitat differentiation among *C. levisecta* source populations and potential recovery sites (Kruskal 1964, Mather 1976). Vegetation cover values were averaged within sites, which may result in unnaturally high values of species richness (McCune and Grace 2002), but was necessary for site-to-site comparisons. The “slow and thorough” autopilot mode setting was used in PC-ORD v. 4.25 (McCune and Mefford 1999) to ordinate *C. levisecta* sites in plant species space. Soil variable vectors that were highly correlated (r^2>0.3) with axes were overlaid on top of the ordination to help explain variation among axes. The significance level was set at $P = 0.05$ prior to statistical analysis.

Results

Characterization of Vegetation Communities

Puget Trough indicator species were primarily perennial species, including native forbs as well as introduced weeds and grasses (Table 2). Native perennials that commonly occurred in low abundance (≤ 7%) at Puget Trough sites included *Pteridium aquilinum*, *Camassia quamash*, *Cerastium arvense*, *Mahonia aquifolium*, *Rosa nutkana*, *Achillea millefolium*, *Lomatium utriculatum*, and *Fritillaria affinis*. *Festuca rubra*, a fine-leaved perennial grass, occurred in moderate abundance (15% - 30%) at the Whidbey Island populations (i.e., Ebey's Landing, Forbes Point, and West Beach). However, it is unknown whether this species is native or introduced to this area (Chappell and Caplow 2004). *Poa pratensis*, an introduced grass, was present at all Puget Trough sites but was particularly abundant at Forbes Point (37.5%). The introduced perennial forb *Plantago lanceolata* was present at all sites with low to moderate abundance (0.3%- 12.5%). Other introduced species that were generally present in low abundance include perennial forbs *Hypochaeris radicata*, *Rumex acetosella*, and *Taraxicum officinale*. *Trifolium dubium* was the only annual indicator species among Puget Trough sites.

Most species indicative of Willamette Valley reintroduction sites were exotic forbs and grasses, many of which were annuals (Table 3). The two native indicator species were the perennial grass *Elymus glaucus*, which occurred at most Willamette Valley sites in low abundance (0.2% - 5.7%), and the perennial forb *Microseris laciniata*, which was present at three sites in low abundance (~1%). Annual non-native grasses were common at Willamette Valley sites. *Bromus hordeaceus* and *Vulpia bromoides* were prevalent but were particularly abundant at the degraded reintroduction sites Sandy River Delta and Starck (>10%). Other exotic annual grasses common to Willamette Valley sites included *Aira caryophyllea,* which was present in low abundance at most sites (<3%), and *Bromus sterilis*, which was particularly common at sites within the Baskett Slough National Wildlife Refuge (0.7% - 7%). The introduced perennial grass, *Arrhenatherum elatius*, occurred at half the sites with moderate cover (8.0% - 26.3%). Common annual weeds characteristic of disturbed sites that were present at half or more Willamette Valley sites included

TABLE 2. Puget Trough indicator species and absolute mean cover values for each site. Exotic species are indicated with [e]. The origin of *Festuca rubra* in this region is unknown. (* denotes an experimental common garden site in Puget Trough)

Species	Indicator Value	Puget Trough Sites					
		EBY	FOR	ROC	TRL	WEB	KAH*
Pteridium aquilinum	78.6	1.0	0.2	7.0	0.7	5.0	7.0
Poa pratensis[e]	70.1	2.0	37.5	1.5	3.1	3.0	1.3
Plantago lanceolata[e]	65.7	8.0	12.5	0.3	7.7	10.0	4.3
Hypochaeris radicata[e]	56.0	1.0	0.2	1.5	1.7	0.0	4.0
*Rumex acetosella*e	51.9	6.0	0.5	0.2	0.3	0.3	5.3
Camassia quamash	50.0	0.0	0.0	2.3	6.7	0.0	3.7
Cerastium arvens[e]	50.0	3.0	0.0	0.2	0.3	0.0	0.0
Mahonia aquifolium	50.0	5.0	0.7	0.0	3.7	0.0	1.0
Rosa nutkana	50.0	0.0	0.2	0.0	1.3	2.0	2.3
Trifolium dubium[e]	50.0	0.0	2.5	0.2	0.0	0.0	1.7
Achillea millefolium	44.9	1.0	1.7	0.8	0.2	0.3	0.0
Lomatium utriculatum	44.8	0.3	0.0	0.0	1.9	0.0	5.7
Anthoxanthum odoratum[e]	42.9	0.0	0.0	9.3	1.7	8.0	0.0
Festuca rubra	42.9	30.0	15.0	0.0	3.3	20.0	0.0
Fritillaria affinis	42.9	0.0	0.0	0.1	1.3	1.0	0.1
Taraxacum officinale[e]	42.9	0.0	0.7	0.8	0.0	0.3	0.1

TABLE 3. Willamette Valley reintroduction site indicator species and absolute mean cover values for each site. Exotic species are indicated with [e].

Species	Indicator Value	Willamette Valley Sites							
		BS1	BB2	BB3	BEL	HER	PIG	SRD	STK
Cerastium glomeratum[e]	79.4	3.0	0.5	0.3	0.2	2.3	0.3	0.0	0.3
Myosotis discolor[e]	68.5	0.2	0.3	0.3	0.0	0.3	0.3	0.0	0.3
Sherardia arvensis[e]	61.2	0.0	3.0	2.7	3.0	0.0	0.3	0.0	0.3
Arrhenatherum elatius[e]	54.2	15.0	8.0	17.3	0.0	0.0	36.3	0.0	0.0
Bromus hordeaceus[e]	52.8	0.0	0.7	9.0	0.0	0.0	4.8	43.3	24.3
Cirsium vulgare[e]	50.9	0.4	0.3	0.0	0.0	1.0	1.5	0.0	1.3
Daucus carota[e]	49.9	0.7	8.3	10.0	0.3	0.0	6.5	0.0	0.3
Aira caryophyllea[e]	48.0	1.3	1.4	1.4	0.0	0.0	0.0	2.4	1.3
Bromus sterilis[e]	45.8	4.0	0.7	7.0	0.0	0.0	1.8	0.0	0.0
Elymus glaucus	45.2	0.0	5.7	3.0	3.5	0.2	3.8	0.0	0.0
Medicago lupulina[e]	41.7	2.2	0.3	0.0	0.2	0.0	0.0	0.0	3.0
Vicia sativa[e]	40.2	0.0	0.3	0.3	11.0	0.0	5.0	0.0	0.3
Microseris laciniata	37.5	0.0	0.0	1.0	1.0	0.0	1.1	0.0	0.0
Veronica spp.[e]	37.5	0.0	0.0	0.0	0.3	0.0	0.3	0.0	0.3
Vulpia bromoides[e]	36.3	0.0	0.7	0.5	0.0	0.0	0.0	15.0	12.0

Cerastium glomeratum, *Myosotis discolor*, *Sherardia arvensis*, and *Medicago lupulina* ($\geq$3%). Frequently encountered exotic perennial forbs were *Vicia sativa*, *Cirsium vulgare*, and *Daucus carota*, which were present at most sites with low to moderate cover (0.7% - 10%).

The majority of species shared by Puget Trough and Willamette Valley sites were introduced species prevalent throughout the Pacific Northwest (Table 4). Several non-native perennial grasses frequently encountered in both ecoregions include *Holcus lanatus* (0.1% - 4.0%), *Dactylis glomerata* (0.1 – 11.0%), and *Poa pratensis* (0.1% - 37.5%), which was present at all but two sites. Annual exotic grasses prevalent at *C. levisecta* populations and experimental reintroduction sites were *Aira caryophyllea* and *Bromus hordeaceus*, and they generally occurred in low abundance except at a few Willamette Valley sites. *Luzula comosa* was the only native graminoid that occurred at most sites, but contributed little to total cover values (usually <1%). Exotic perennial forbs were the predominant functional group common among Puget Trough and Willamette Valley sites, and included the following species: *Plantago lanceolata*, *Vicia hirsuta*, *Vicia sativa*, *Cerastium glomeratum*, *Hypochaeris radicata*, *Rumex acetosella*, *Daucus carota*, and *Hypericum perforatum*. Two native perennial forbs common to both regions were *Achillea millefolium* and *Eriophyllum lanatum*, which usually occurred in low abundance (<2%). In general, Puget Trough sites had greater native species richness ($\bar{x}$ = 21.2 ± 3.6), and fewer exotic species ($\bar{x}$ =15.3 ± 1.1), than Willamette Valley sites ($\bar{x}$ = 15.1 ± 2.9 and $\bar{x}$ =19.2 ± 2.0, respectively).

Characterization of Soils

Soils from Puget Trough and Willamette Valley sites were generally distinct, although they shared some qualities (Table 5, Table 6). Acidic soils dominate remaining *C. levisecta* populations and reintroduction sites (pH= 4.68 - 5.75), and in general, Puget Trough and Willamette Valley soils had similar levels of NH_4, NO_3, TN, and TOC. Rocky Prairie, Kah Tai Prairie, and Heritage Seedling had particularly high levels of NH_4, NO_3, and TN. The carbon to nitrogen ratio from all sites was low (6.4 - 12.6), and organic matter content was generally high (3.9 % - 15.6%). Puget Trough sites with particularly black soils, rich in organic matter (12.9% - 15.6%) included Trial Island, Rocky Prairie, and Kah Tai Prairie.

Puget Trough soils generally had higher levels of sulfur and magnesium than Willamette Valley soils. Sulfur levels were particularly high at Trial Island (434.9 µg/g) and Rocky Prairie (325.3 µg/g), and generally appear to be positively correlated with organic matter content. Sites situated on coastal bluffs and prairies had higher concentrations of magnesium (2591.0 µg/g - 3615.5 µg/g) than inland sites (1022.3 µg/g - 2454.5 µg/g).

TABLE 4. Species and cover values (%) occurring at half or more of the 14 *C. levisecta* sites. Cover values were averaged among plots at each site. Species richness and constancy (i.e., percentage of sites where the species occurred) were calculated at the site level. Exotic species are indicated with [e]. (* denotes an experimental common garden site in Puget Trough)

		Puget Trough Sites						Willamette Valley Sites							
Species	Constancy	EBY	FOR	ROC	TRL	WEB	KAH*	BS1	BB2	BB3	BEL	HER	PIG	SRD	STK
Poa pratensis[e]	85.7	2.0	37.5	1.5	3.1	3.0	1.3	3.3	0.3	0.3	0.7	0.0	0.1	0.0	2.3
Achillea millefolium	71.4	1.0	1.7	0.8	0.2	0.2	0.0	0.0	0.1	0.3	1.0	0.3	1.1	0.0	0.0
Plantago lanceolata[e]	71.4	8.0	12.5	0.3	7.7	10.0	4.3	0.0	2.0	0.8	0.7	0.0	0.0	0.8	0.0
Vicia hirsuta[e]	71.4	0.3	2.5	0.0	0.8	5.0	0.0	2.0	0.3	0.8	0.3	0.0	0.3	0.0	0.3
Vicia sativa[e]	71.4	0.3	1.5	0.0	1.5	0.3	0.3	0.0	0.3	0.3	11.0	0.0	5.0	0.0	0.3
Aira caryophyllea[e]	64.3	0.3	0.3	0.1	0.0	0.0	0.2	1.3	1.4	1.4	0.0	0.0	0.0	2.4	1.3
Bromus hordeaceus[e]	64.3	0.3	0.5	0.0	0.1	0.0	0.8	0.0	0.7	9.0	0.0	0.0	4.8	43.3	24.3
Cerastium glomeratum[e]	64.3	0.0	0.2	0.0	0.0	0.0	0.1	3.0	0.5	0.3	0.2	2.3	0.3	0.0	0.3
Holcus lanatus[e]	64.3	0.0	3.0	0.1	0.0	4.0	0.0	0.1	0.8	0.0	0.3	0.7	0.8	0.1	0.0
Hypochaeris radicata[e]	64.3	1.0	0.2	1.5	1.7	0.0	4.0	0.0	1.4	0.0	0.3	0.0	0.0	0.2	2.0
Luzula comosa	64.3	1.0	0.7	0.1	0.3	0.0	0.0	0.0	0.3	0.2	1.0	0.0	0.2	0.2	0.0
Rumex acetosella[e]	64.3	6.0	0.5	0.2	0.3	0.3	5.3	0.0	0.0	0.0	6.0	0.0	0.0	4.0	1.3
Daucus carota[e]	57.1	0.3	4.0	0.0	0.0	0.0	0.0	0.7	8.3	10.0	0.3	0.0	6.5	0.0	0.3
Hypericum perforatum[e]	57.1	0.0	0.0	1.4	0.0	0.0	0.1	0.7	0.3	0.1	0.2	0.3	0.3	0.0	0.0
Dactylis glomerata[e]	50.0	1.0	0.5	0.0	0.1	0.3	11.0	0.0	8.0	0.0	0.0	0.0	0.0	0.0	0.7
Eriophyllum lanatum	50.0	1.0	0.0	4.6	0.3	0.0	0.1	0.0	0.8	2.3	0.0	0.1	0.0	0.0	0.0
Myosotis discolor[e]	50.0	0.0	0.0	0.0	0.0	0.3	0.0	0.2	0.3	0.3	0.0	0.3	0.3	0.0	0.3
native species richness	-	17	12	33	31	15	19	9	21	17	19	26	20	3	6
exotic species richness	-	11	23	20	14	11	13	18	22	21	17	17	19	14	24

TABLE 5. Puget Trough mean soil values. Soil texture was abbreviated; C= clay, L= loam, S= sand. (* denotes an experimental common garden site in Puget Trough)

	Puget Trough Sites					
soil trait	EBY	FOR	ROC	TRL	WEB	KAH*
pH	5.75	5.51	4.88	5.60	5.32	5.42
NH_4 (mg/kg)	7.80	7.03	33.68	13.57	15.92	27.38
NO_3 (mg/kg)	7.00	0.54	10.40	3.89	0.53	7.56
TOC (μg/g)	159.05	220.99	449.69	113.29	253.72	404.33
TN (μg/g)	18.80	17.49	53.51	17.80	25.53	37.83
C:N	8.80	12.64	8.40	6.37	9.94	10.69
%OM	3.89	4.95	13.21	15.56	7.21	12.91
K (μg/g)	529.10	1180.00	457.90	1032.61	635.00	666.70
P (μg/g)	131.80	103.35	402.10	459.44	265.90	336.75
S (μg/g)	102.69	120.00	325.25	434.89	236.55	297.20
Mg (μg/g)	3615.50	2799.50	1780.50	3185.25	2591.00	3446.50
Mn (μg/g)	122.25	180.60	295.45	550.63	356.55	242.75
Db (g/cm^3)	0.84	0.71	0.65	-	0.92	0.64
% sand	87.6	49.7	70.70	56.2	70.1	71.85
% silt	10.8	28.3	22.10	33.1	19.8	21.49
% clay	1.6	22.0	7.30	10.7	10.1	6.66
texture	S	SCL	SL	SL	SL	SL

TABLE 6. Mean soil values for Willamette Valley reintroduction sites. Soil texture was abbreviated; C= clay, L= loam, S = sand, SI= silt

	Willamette Valley Sites								
	BS1	BB2	BB3	BEL	HER	PIG	PMC	SRD	STK
pH	5.40	5.30	5.60	4.87	5.82	5.30	5.25	4.68	4.85
NH_4 (mg/kg)	20.93	14.37	16.18	14.61	30.60	21.98	9.21	9.93	16.34
NO_3 (mg/kg)	3.29	1.74	1.90	4.24	9.79	2.87	4.50	9.91	8.49
TOC (μg/g)	299.48	188.48	210.12	297.35	276.79	206.80	122.66	151.73	193.71
TN (μg/g)	27.66	17.54	17.79	27.35	34.07	25.98	15.63	20.68	21.95
C:N	10.83	10.74	11.81	10.87	8.12	7.96	7.85	7.34	8.82
%OM	6.99	7.58	5.76	8.41	8.05	8.14	4.32	5.17	7.36
K (μg/g)	1606.50	1517.50	2496.00	1470.00	815.05	1020.65	1569.50	453.40	1419.50
P (μg/g)	165.15	107.10	126.00	260.85	629.35	430.85	448.40	480.70	348.00
S (μg/g)	159.05	137.65	131.00	128.15	155.20	128.65	65.99	167.85	119.75
Mg (μg/g)	1802.00	2147.50	2453.50	1022.25	1029.00	1350.50	2118.00	1030.80	2111.00
Mn (μg/g)	281.30	171.55	155.50	325.10	770.95	534.65	390.60	87.57	473.35
D_b (g/cm^3)	0.82	0.85	0.81	0.87	0.98	0.91	1.25	0.91	0.94
% sand	16.72	19.19	20.86	19.76	28.02	16.27	12.33	64.12	12.30
% silt	45.63	41.87	38.48	33.94	44.57	37.69	52.10	28.67	48.71
% clay	37.65	38.94	40.66	46.30	27.41	46.05	35.57	7.22	38.98
texture	SICL	SICL	SICL	C	CL	C	SIC	SL	SIC

Willamette Valley sites generally had higher concentrations of potassium and phosphorous than Puget Trough sites, although there was a lot of variability among sites from each region. Soil texture most clearly distinguished the two regions. Sand was a larger component of Puget Trough soils (49.7% - 87.6%) than Willamette Valley soils (12.3% - 28.0%), excluding Sandy River Delta, which had a high sand component (64.1%). Willamette Valley sites were primarily dominated by silt (33.9% - 52.1%) and clay (27.4% - 46.3%). The sandy Puget Trough soils generally had lower bulk density (0.64 - 0.92) than the heavy clay soils of the Willamette Valley (0.81 - 1.25).

Regional Patterns in Habitat Characteristics

Regional divergence between Willamette Valley and Puget Trough sites was apparent along axis

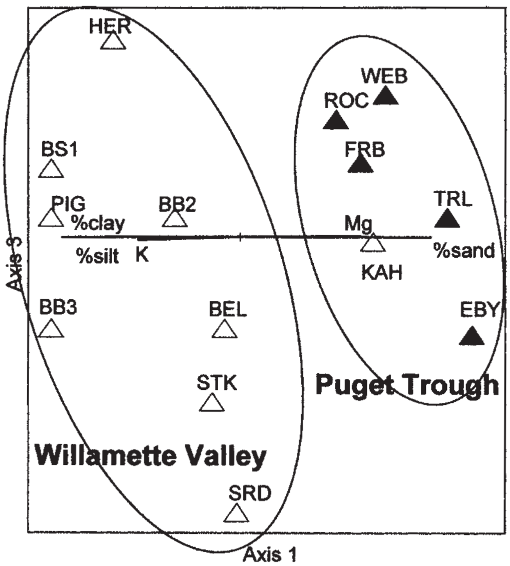

Figure 2. NMS solution of sites in species space with soil variable overlays. Each point represents a site (source population = ▲, common garden sites= △). Soil variables strongly associated with vegetation community composition are indicated with vector overlays (r^2 >0.3). The length of the vector indicates the strength of the relationship of a variable with the ordination scores. Soil texture best explains differences in community composition with sites from the Willamette Valley and Puget Trough aggregating at opposite sides of axis 1. See Table 1 for site abbreviations.

1 of a 3-D NMS solution that explained 66% of the variation in the original data (Figure 2). The final configuration had lower stress than those found with Monte Carlo randomizations (P = 0.020). Axes 1 and 3 together explained half of the variability in community composition (r^2= 0.24, 0.25, respectively), and axis 2 explained another 17%. Axes 1 and 3 are displayed, as these axes accounted for the majority of variation in community composition. Sites separated regionally in the ordination space and circles were drawn around sites from the two ecoregions. Correlations of soil variables with axis 1 help explain the regional divergence in vegetation communities. Soil texture, as well as potassium and magnesium concentrations, were strongly associated with axis 1 (r^2= 0.38 - 0.72). Ordinations were rotated to align with percentage sand, which had the strongest relationship (r^2= 0.72) with axis 1. None of the measured soil variables were correlated with the variation in plant communities along axis 3.

Discussion

Plant communities differed considerably among sites from the northern and southern portions of *C. levisecta*'s historic range. Puget Trough and Willamette Valley sites had distinct species assemblages likely related to ecoregional differences in geology, climate, ocean proximity, and land-use history. Although sites from these two regions did share some species in common (Table 4), the majority of these were invasive exotics that are widespread throughout the Pacific Northwest. *Poa pratensis*, an introduced perennial grass, was particularly common in our study, occurring at all but two sites. This species is a problematic invader of Pacific Northwest prairies because it has the capacity to recruit by tillering in dense above-ground litter layers that result in the absence of fire (MacDougall and Turkington 2004). Nearly half of the Puget Trough indicator species were native perennials, while almost all species indicative of Willamette Valley sites were exotic, annual forbs and grasses. Puget Trough sites also had greater native species richness than those of the Willamette Valley, which in turn generally had higher numbers of exotic species. Invasion by exotic species is a major threat to the viability of remaining *C. levisecta* populations (Caplow 2004) and management of non-native species will clearly be an important component of reintroduction efforts in the Willamette Valley. The common functional groups at remaining *C. levisecta* populations (i.e., native perennials) and reintroduction sites in the Willamette Valley (i.e., introduced annuals) highlight important differences in community structure among sites that we sampled from these two ecoregions.

Castilleja levisecta sites from the Puget Trough had distinctly different soils than the reintroduction sites in the Willamette Valley, but did share some commonalities. All *C. levisecta* sites were acidic with abundant organic matter, and generally had low carbon to nitrogen ratios, which is characteristic of graminoid dominated soils (Brady and Weil 2002). Several soil characteristics, including texture and levels of potassium and magnesium, were strongly associated with differences in community composition between the two ecoregions (Figure 2). *Castilleja levisecta* sites in the Puget Trough were found primarily on sandy coastal prairies influenced by sea spray, whose salts are often dominated by sulfates and chlorides of calcium, magnesium, and sodium (Brady and Weil 2002). The higher magnesium content observed at Puget Trough sites ($\bar{x}$ = 2903.0 µg/g ± 273.9) compared to Willamette Valley sites ($\bar{x}$ = 1673.8 µg/g ± 201.4) was likely due to their vicinity to marine environments and may influence species composition. Willamette Valley sites were typically situated in upland prairies dominated by silty-clay soils with relatively high levels of potassium ($\bar{x}$ = 1374.3 µg/g ± 204.2). The lower levels of potassium we observed at Puget Trough sites ($\bar{x}$ = 750.2 µg/g ± 118.2) is consistent with their high sand content (Brady and Weil 2002). Our soil analyses are similar to Chappell & Caplow's (2005) characterization of remaining *C. levisecta* populations, who found Puget Trough soils to be generally high in magnesium and sand content, with low clay percentage and potassium concentrations.

Historical references to collections from moist sites suggest a wider habitat preference than strictly well-drained soils. A shortcoming of our study is that we did not characterize moist *C. levisecta* reintroduction sites in the Willamette Valley. Additionally, a portion of the San Juan Valley extant population inhabits a wet swale which supports wetland vegetation and soils (Chappell and Caplow 2004). This is the only known wetland site that currently supports *C. levisecta.* Further examination of *C. levisecta* habitat suitability should investigate the ability of wet prairie habitat to support *C. levisecta* reintroduction endeavors in the Willamette Valley.

Only 2.6% of pre-settlement, native dominated grasslands in the Puget Lowland are estimated to remain (Chappell et al. 2000), and less is suspected to remain in the Willamette Valley, OR. Although a mapping effort by Chappell et al. (2000) showed low *C. levisecta* co-occurrence with pre-settlement grassland soil and vegetation polygons, it was likely because the minimum map unit employed in the study was larger than the size of most of the remaining *C. levisecta* populations. This emphasizes the degree of habitat fragmentation and alteration that extant *C. levisecta* populations have been subjected to and suggests that remaining populations likely represent only a fraction of the site characteristics *C. levisecta* once inhabited. Furthermore, remaining populations appear to be relegated to habitat unsuitable for agriculture (e.g., too steep, too rocky, and/or too much sea spray influence). Efforts to reestablish species in portions of their historic range need to consider the ecological and cultural processes that once determined species occurrence (MacDougall et al. 2004). For example, fire initiated by Native Americans historically played an integral role in maintaining prairie vegetation in the Pacific Northwest and mounting evidence suggests that *C. levisecta* responds favorably to fire (Dunwiddie et al. 2000). Successful reintroduction of *C. levisecta* may necessitate a fire regime that emulates historical conditions.

Castilleja levisecta recovery site selection may be especially challenging in the southern portion of the species' historic range because prospective planting sites are ecologically distant from Puget Trough seed sources. Maximizing the ecological similarity, in terms of species composition and soil characteristics, between existing populations and prospective reintroduction sites within the Puget Trough ecoregion may be appropriate because sites share similar floras and geologic histories. Using reciprocal transplant experiments in Southern California, Montalvo & Ellstrand (2000) found that the cumulative fitness of *Lotus scoparius* decreased with increasing environmental distance, emphasizing the importance of matching seed sources with ecologically similar restoration sites within a given region. However, large differences in species composition between ecoregions make standard predictions untenable. In order to be useful at great ecological distances where floras are distinct, a different metric of ecological similarity is needed.

We suggest using a functional group approach to compare plant communities among sites from distinct ecoregions. Functional groups are useful in comparative studies of communities, enabling the comparison of species that share ecological characteristics and play similar roles in communities, but are taxonomically distinct (Simberloff and Dayan 1991, Voigt and Perner 2004). Species could be assigned to functional groups based on life history characteristics (annual vs. perennial), origin (native vs. exotic), and habit (graminoid, forb, or woody). We predict that plant functional groups will be a useful method to measure habitat similarity and determine suitable recovery sites across large ecological and geographic distances where floristic communities differ.

Acknowledgements

We would like to thank USFWS *Castilleja levisecta* Recovery Team and the Institute for Applied Ecology for technical and logistical support. We appreciate contributions from Chris Chappell of the Washington Department of Natural Resources who provided source population vegetation data, and Matt Fairbarnes of Aruncus Consulting who collected soil samples from Trial Island, B.C. Thanks to Machelle Nelson who shared her expertise and time during our soil analysis. Funding for this study was provided by USFWS contract 101813M465, a National Science Foundation Graduate Research Fellowship, a Native Plant Society of Oregon Field Grant, and Bonnie Templeton Award for Plant Systematics.

Literature Cited

Bowles, M., R. Flakne, K. McEachern, and N. Pavlovic. 1993. Recovery planning and reintroduction of the federally threatened pitcher's thistle (*Cirsium pitcheri*) in Illinois. Natural Areas Journal 13:164-176.

Boyd, R. 1986. Strategies of Indian burning in the Willamette Valley. Canadian Journal of Anthropology **5**:65-86.

Brady, N. C., and R. R. Weil. 2002. The Nature and Property of Soils, 13 edition. Prentice Hall, Upper Saddle River, N.J.

Caplow, F. 2004. Reintroduction plan for golden paintbrush (*Castilleja levisecta*). Washington Natural Heritage Program, Department of Natural Resources, Olympia, WA.

Chappell, C. B., and F. Caplow. 2004. Site characteristics of golden paintbrush populations. Washington Natural Heritage Program, Department of Natural Resources, Olympia, WA.

Chappell, C. B., M. M. Gee, B. Stephens, R. Crawford, and S. Farone. 2000. Distribution and decline of native grasslands and oak woodlands in the Puget Lowland and Willamette Valley ecoregions, Washington. Pages 223 *in* S. H. Reichard, P. Dunwiddie, J. Gamon, A. Kruckeberg, and D. Salstrom, editors. Proceedings from a Conference of the Rare Plant Care & Conservation Program of the University of Washington, Seattle, WA.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345-366.

Dunwiddie, P., R. Davenport, and P. Speaks. 2000. Effects of burning on *Castilleja levisecta* at Rocky Prairie Natural Area Presearve, Washington: A summary of three long-term studies. *in* S. H. Reichard, P. Dunwiddie, J. Gamon, A. Knuckeberg, and D. Salstrom, editors. Conservation of Washington's Rare Plants and Ecosystems. Washington Native Plant Society, Seattle, WA.

Fiedler, P. L., and R. D. Laven. 1996. Selecting reintroduction sites. *in* D. A. Falk, C. I. Millar, and M. Olwell, editors. Restoring Diversity. Island Press, Washington, D.C.

Franklin, J. F., and C. T. Dyrness. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press.

Gamon, J. 1995. Report on the status of *Castilleja levisecta*. Washington Natural Heritage Program, Department of Natural Resources, Olympia, WA.

Guerrant, E. O. 1996. Designing populations: demographic, genetic, and horticultural dimensions. Pages 171-208 *in* D. A. Falk, C. J. Millar, and M. Olwell, editors. Restoring Diversity. Island Press, Washington, D.C.

Guerrant, E. O., Jr., and B. M. Pavlik. 1998. Reintroduction of rare plants: genetics, demography, and the role of ex situ conservation methods. Pages 80-108 *in* P. L. Fiedler and P. M. Kareiva, editors. Conservation Biology: for the Coming Decade. Chapman & Hall, New York.

Huenneke, L. F. 1991. Ecological implications of genetic variation in plant populations. *In* D. A. Falk and K. Holsinger, editors. Genetics and Conservation of Rare Plants. Oxford University Press, New York.

Hufford, K. M., and S. J. Mazer. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. Trends in Ecology and Evolution 18:147-155.

IUCN. 1998. Guidelines for re-introductions. Prepared by the IUCN (World Conservation Union)/Species Survival Commission Re-introduction Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika:115-129.

Lawrence, B. A. 2005. Studies to facilitate the reintroduction of golden paintbrush (*Castilleja levisecta*) to the Willamette Valley, Oregon. M.S. Thesis. Oregon State University, Corvallis, Oregon.

MacDougall, A. S., B. R. Beckwith, and C. Y. Maslovat. 2004. Defining conservation strategies with historical perspectives: a case study from a degraded oak grassland ecosystem. Conservation Biology 18:455-465.

MacDougall, A. S., and R. Turkington. 2004. Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. Journal of Ecology **92**.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. J. Wiley & Sons, London.

McCune, B., and J. B. Grace. 2002. Analysis of Ecological Communities. MJM Software Design, Glenden Beach, OR.

McCune, B., and M. J. Mefford. 1999. Multivariate Analysis of Ecological Data. *In* MjM Software, Gleneden Beach, Oregon, U.S.A.

McKay, J. K., C. E. Christian, S. Harrison, and K. J. Rice. 2005. "How local is local?"—a review of practical and conceptual issues in the genetics of restoration. Restoration Ecology **13**:432-440.

Montalvo, A. M., and N. C. Ellstrand. 2000. Transplantation of the subshrub *Lotus scoparius*: Testing the Home-Site Advantage Hypothesis. Conservation Biology 14:1034-1045.

Pavlik, B. M., A. M. Howald, and D. L. Nickrent. 1993. The recovery of an endangered plant. I. Creating a new population of *Amsinckia grandiflora*. Conservation Biology 7:510-526.

Simberloff, D., and T. Dayan. 1991. The guild concept and the structure of ecological communities. Annual review of ecology and systematics 22:115-143.

U.S.F.W.S. 2000. Recovery plan for golden paintbrush (*Castilleja levisecta*). *in*. U.S. Fish and Wildlife Service, Portland, OR.

Received 26 December, 2005
Accepted for publication 3 May, 2006

USDA-NRCS. 2006. The PLANTS Database, 6 March 2006 (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.

Voigt, W., and J. Perner. 2004. Functional group interaction patterns across trophic levels in a regenerating and seminatural grassland. *In* V. M. Temperton, R. J. Hobbs, T. Nuttle, and S. Halle, editors. Assembly Rules and Restoration Ecology: Bridging the Gap between Theory and Practice. Island Press, Washington.