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DIRECT AND INDIRECT EFFECTS OF HOST PLANTS: IMPLICATIONS FOR REINTRODUCTION OF AN ENDANGERED HEMIPARASITIC PLANT (*CASTILLEJA LEVISECTA*)

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ABSTRACT

Rare, parasitic plants pose an interesting challenge to restoration practitioners. In addition to the problems associated with small population size, rare parasites may also be limited by their host requirements. We examined how the performance of a rare Pacific Northwest hemiparasite, *Castilleja levisecta*, was affected by the availability of different host combinations in the greenhouse and in the field. *Castilleja levisecta* individuals were grown with two individuals of the grass *Festuca roemeri*, two individuals of the aster *Eriophyllum lanatum*, one individual of each of these species (a "mixed" treatment), or without any host. We did not find support for the complimentary diet hypothesis, which predicts that parasites grown with multiple host species perform better than individuals grown alone or with a single host. In the greenhouse, *C. levisecta* individuals grown in the mixed treatment had greater stem growth than those planted with *F. roemeri*, but did not differ from *E. lanatum* or no-host treatments. In the field, vole activity had indirect effects on *C. levisecta* survival mediated through host species: vole tunneling and *C. levisecta* mortality were strongly associated with host treatments including *E. lanatum*. Vole tunneling and *C. levisecta* mortality were strongly associated with host treatments including *E. lanatum*. Field survival of no-host and *F. roemeri* treatments were significantly higher than those grown with *E. lanatum*. Our results emphasize the importance of basing conservation decisions on experimental research conducted under conditions similar to those of the intended application, as greenhouse results were a poor predictor of field performance. For restoration of endangered hemiparasitic plants, we recommend planting with hosts that are not attractive to herbivores.

Key Words: *Castilleja levisecta*, complimentary diet hypothesis, host-use, rare hemiparasite, reintroduction.

Parasitic plants are a dynamic component of many plant communities capable of altering productivity (Marvier 1998b; Matthies 1997), competitive interactions (Gibson and Watkinson 1991; Matthies 1996), and community structure (Gibson and Watkinson 1992; Press 1998). Although many parasitic plants are agricultural pests, some are of conservation concern and pose an interesting challenge to restoration practitioners (Marvier and Smith 1997). In addition to the diversity of obstacles typically encountered during reintroduction, rare parasites may also be limited by host requirements. Uncertainties associated with parasite host specificity and the availability and quality of hosts at restoration sites are likely to impede parasitic plant reintroduction efforts (Marvier and Smith 1997). Therefore, successful management of rare parasites necessitates consideration of their unique biology. We conducted greenhouse and field experiments with *Castilleja levisecta* Greenman (golden paintbrush), a rare hemiparasite endemic to the prairies of the Pacific Northwest of the United States, to evaluate its host preferences in support of recovery actions.

Although facultative hemiparasites are photosynthetic and do not require a host plant, they often form haustoria (i.e., physical connections with other root systems) through which nutrients, water, and secondary compounds are obtained from the host (Kuijt 1969; Press 1989). In natural systems, unattached mature facultative parasites are uncommon, and attachment to a host generally stimulates parasite fitness and growth (Kuijt 1969). Most members of the genus *Castilleja* are considered generalist hemiparasites, capable of parasitizing multiple host species (Dobbins and Kuijt 1973; Heckard 1962). However, the degree to which a host stimulates hemiparasite fitness varies considerably among host species (Chuang and Heckard 1971; Gibson and Watkinson 1992; Marvier 1998b; Matthies 1996, 1997; Seel and Press 1993). Interactions between plant parasites and host species can have direct and indirect effects both on host and parasite performance, as well as their pollinators (Adler et al. 2001), and herbivores (Adler 2002, 2003; Adler et al. 2001; Marko 1996; Marvier 1996). Parasitic plants can acquire secondary compounds from host species (Govier et al. 1967; Schneider and Stermitz 1990; Stermitz and Harris

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1987), which in turn can alter species interactions. For example, acquisition of alkaloids from the host *Lupinus albus* directly reduced insect herbivory of *Castilleja indivisa*, and indirectly increased pollination (Adler et al. 2001).

In the field, hemiparasitic plants often parasitize several hosts simultaneously (Gibson and Watkinson 1989; Matthies 1996). Generalist hemiparasites may perform better on a mixed diet relative to a homogenous diet due to improved nutrient balance and/or dilution of toxic secondary plant compounds (Marvier 1998a). Many taxa benefit from multiple food sources, including some insects (Bernays et al. 1994), gastropods (Pennings et al. 1993), and reptiles (Bjorndal 1991). Therefore, we propose that providing multiple nutrient sources increases individual fitness (the complimentary diet hypothesis). We test this hypothesis by comparing the size and survival of a rare hemiparasitic plant in mixed host, single host, and no-host plantings.

Castilleja levisecta is a federally threatened species and is currently restricted to eleven populations in the Pacific Northwest. The species is extinct in the southern portion of its historic range, including the Willamette Valley, Oregon. Federal recovery criteria for *C. levisecta* call for the existence of 20 populations composed of 1000 flowering individuals (USFWS 2000). However, the species has limited capacity for natural dispersal and colonization of new sites, necessitating *ex situ* conservation techniques to meet recovery goals. Thus, a strategic reintroduction plan has been prepared to support the long-term viability of *C. levisecta* and requires the establishment of new populations within its historic range (Caplow 2004). Although several studies have investigated *C. levisecta* host use (Pearson and Dunwiddie 2006; Wayne 2004; Wentworth 2001), clarification of its host dynamics in a restoration context is necessary before large scale reintroduction efforts are pursued.

While *C. levisecta* does not require a host to reproduce in a greenhouse environment and does not appear to be host specific (Wentworth 2001), evidence suggests planting *C. levisecta* in the field with a perennial host increases size and reproductive output (Pearson and Dunwiddie 2006; Wayne 2004). Greenhouse observations suggest that *C. levisecta* can form haustorial connections with several perennial prairie species [e.g., *Leucanthemum vulgare* Lam., *Eriophyllum lanatum* (Pursh) Forbes, *Festuca roemeri* (Pavlick) Alexeev, and *Fragaria vesca* L.], and with itself when grown alone (Kaye 2001; Wentworth 2001). Field experiments indicate that outplanting *C. levisecta* with *F. roemeri* increases the number of inflorescences produced compared to no-host controls, although host presence did not affect field survival rates (Wayne 2004). In addition, *C. levisecta* is frequently eaten by small mammals (Caplow 2004; Wayne 2004), but host-mediated effects of herbivory on the species has not previously been evaluated.

Here, we use greenhouse and field studies to test the complimentary diet hypothesis and examine how host-interactions affect herbivory by rodents under field conditions, as well as provide recommendations for future *C. levisecta* recovery efforts.

Methods

Study species

Castilleja levisecta (Orobanchaceae, formerly classified in Scrophulariaceae) is a short-lived (5–6 yr), multi-stemmed, perennial endemic to the native grasslands of the Western Pacific Northwest United States. It is an out-crossing species primarily pollinated by *Bombus* spp. and is known only to reproduce by seed (Kaye and Lawrence 2003; Wentworth 2001). The eleven remaining *C. levisecta* populations are concentrated in the San Juan Archipelago of the Puget Trough eco-region, and are found on sandy, well drained soils of glacial origin (Chappell and Caplow 2004). Despite the rarity of this species, the remaining populations maintain unusually high levels of genetic diversity compared with other endemic species and members of the Orobanchaceae (Godt et al. 2005).

Greenhouse experiment

To test for differences in *C. levisecta* performance when grown with different host combinations, we randomly assigned individuals to one of four host treatments, including no-host (control), two *E. lanatum* (Asteraceae) individuals, two *F. roemeri* (Poaceae) individuals, or one individual of each of these host species (''mixed''). We used plant material from two *C. levisecta* source populations located on Whidbey Island, WA (Ebey's Landing: 48°13′35″N, 122°46′00″W and Forbes Point: 48°16′15″N, 122°37′35″W). Approximately twenty host treatment replicates from each of these source populations were used to test our hypotheses, for a total of 39 replicates per host treatment (n = 156). *Eriophyllum lanatum* and *F. roemeri* were used as host plants because *C. levisecta* forms haustorial connections with these native perennials (Wayne 2004, Beth Lawrence, pers. obs.), they are common at southern extant populations (Chappell and Caplow 2004), and are likely to be present at reintroduction sites.

Castilleja levisecta capsules were collected from 17 maternal plants from each of the two source populations in August 2003 to provide seeds for this experiment and were germinated using the methods outlined in Lawrence and Kaye (2005).

On 1 December 2003, *C. levisecta* germinants were planted into cell flats in a well-drained medium amended with slow release micro- and macro- nutrients and were placed in a greenhouse with 400 watt high pressure sodium lights and temperature fluctuating every 12 hr (12°C /18°C). A randomized block design was implemented to assign host treatments to *C. levisecta* individuals, with source population and maternal line serving as the blocking factors. Two maternal lines from Ebey's Landing and three from Forbe's Point were assigned to two blocks, because extra plants from these maternal lines were available. Plants were repotted into 3.8 L pots with their assigned host treatment on 28 January 2004. *Castilleja levisecta* individuals and potential hosts were planted in a triangle with all plants 10 cm apart; *C. levisecta* individuals assigned the no-host treatment were planted in the center of the pot. We used a no-host control rather than planting three *C. levisecta* individuals together because we had a limited number of plants. *Eriophyllum lanatum* plants were rooted cuttings from Willamette Valley genetic stock provided by Heritage Seedling Co., Salem, OR. We used *F. roemeri* individuals grown from Willamette Valley seed that were one year old when paired with *C. levisecta*. We attempted to equalize above- and below-ground biomass of provided hosts by trimming them with shears. Plants were randomized on greenhouse benches and fertilized biweekly with a liquid 15-30-15 fertilizer to encourage growth and establishment.

We recorded total stem length, stem number, and number of flowers produced by each *C. levisecta* individual in May 2004, approximately 15 wk after potting the hemiparasites and hosts together. Flowering had finished at this time, so our measurements are considered estimates of total flower production. Plants were moved to a shade-house in June 2004 and received supplemental water throughout the summer.

Field experiment

To test our host and herbivore hypotheses under field conditions, we transplanted the same potted plants with hosts used in the greenhouse study to an upland prairie on 1 December 2004. Our field site was located at Pigeon Butte, Finley National Wildlife Refuge, OR (44°23′54″N, 123°19′11″W), in habitat likely to be used for future *C. levisecta* recovery efforts in the Willamette Valley. The site had a high diversity of native perennials and abundant non-native pasture grasses (e.g., *Festuca arundinacea* Schreb. and *Arrhenatherum elatius* (L.) P. Beauv. ex J. Presl & C. Presl). It was situated on the shoulder of a butte at 150 m elevation, dominated by silty-clay-loam soils. Average annual precipitation in this region is approximately 115 cm, with average annual minimum and maximum temperatures of 5°C and 17°C, respectively (WRCC 2005).

We randomly planted host-parasite replicates (each pot was a replicate) into the center of a 1 m^2 plot within a 10 × 15-m grid fenced to exclude deer. Deer are frequent herbivores of the species and threaten extant populations; fences to exclude deer have been built at two of the extant *C. levisecta* populations (Beth Lawrence, pers. obs.). *Castilleja levisecta* individuals and hosts were dormant at the time of outplanting, and senesced material was removed. A balanced design could not be executed in the field because some greenhouse plants died during the previous summer. However, at least 22 replicates of each of the four host treatments were transplanted into the field (no-host, n = 39; *F. roemeri*, n = 31; *E. lanatum*, n = 26; mixed, n = 22).

Field transplants were monitored in early June 2005 because surveys conducted in a companion 2004 field study revealed that transplants were at their maximum size and peak inflorescence at this time (Lawrence 2005). Vole abundance was unusually high throughout the Pacific Northwest during the 2005 growing season and all surviving *C. levisecta* individuals at the field site were subjected to herbivory, most likely from grey-tailed voles (*Microtus canicaudus*) (Beth Lawrence, pers. obs.). Stem length and/or number, as well as flower and/or seed production were not reliable measures of *C. levisecta* performance, as herbivory appeared to stimulate resprouting, alter plant morphology, and prevent individuals from flowering (Beth Lawrence, pers. obs.). Therefore, we used *C. levisecta* survival as the response variable for the field component of our study. Vole tunneling was also very frequent, indicating herbivore pressure occurred in the root zone as well as above ground. Tunnels were unevenly distributed throughout the study area, so herbivore pressure by voles was measured as presence or absence of tunnels within 15 cm of the transplant root crown.

Statistical analyses

We used multivariate analysis of variance (MANOVA) with a Wilks' lambda multivariate F test to simultaneously test for differences in *C. levisecta* greenhouse response variables (stem length, stem number, and flower number) among host treatments. Prior to MANOVA analysis, stem number was log-transformed to improve homoscedasticity. *Castilleja levisecta* source population and maternal effects were used as blocking factors in this analysis because differential growth among populations and individuals from different maternal lines has been observed in this species (Kaye 2001). However, we focus our analysis on host treatment effects. Following MANOVA, univariate ANOVAs were conducted

TABLE 1. RESULTS FROM UNIVARIATE ANOVAS TESTING THE EFFECT OF HOST TREATMENT (HOST), SOURCE POPULATION (SOURCE), MATERNAL LINE (MATLINE), AND THE HOST TREATMENT*SOURCE POPULATION INTERACTION (HOST*SOURCE) ON THE NUMBER OF *C. LEVISECTA* FLOWERS PRODUCED (FLOWER #), NUMBER OF STEMS (STEM #), AND TOTAL STEM LENGTH (STEM LENGTH) IN THE GREENHOUSE. Significant effects at $\alpha = 0.05$ denoted with *.

RESPONSE	EFFECT	DF	MS	F	P
Flower #	host	3	474	0.84	0.47
	source	1	18313	32.32	<0.001*
	matline	32	877	1.55	0.048*
	host*source	3	38	0.067	0.98
Stem #	host	3	0.24	2.87	0.039*
	source	1	2.61	31.76	<0.001*
	matline	32	0.097	1.19	0.25
	host*source	3	0.0069	0.084	0.97
Stem Length	host	3	7112	3.69	0.014*
	source	1	197	0.10	0.75
	matline	32	3689	1.9	0.0067*
	host*source	3	1879	0.97	0.41

on the three greenhouse response variables. Significant ANOVAs were followed by Tukey's HSD for pairwise comparisons among host treatments.

We used binary logistic regression to test for differences among host treatments in *C. levisecta* field survival and vole tunnel presence. Significance was measured by drop in deviance (DEV) with a chi-square distribution. Dunn-Sidak corrections were used to adjust alpha levels for all pair-wise comparisons among host treatments. We used linear regression to determine if the proportion of transplants with vole tunnels was associated with the proportion of *C. levisecta* individuals surviving. Finally, we calculated an odds ratio to compare *C. levisecta* survival when planted with *E. lanatum* versus survival when not planted with this species (i.e., alone or with *F. roemeri*). All analyses were conducted using S-PLUS v. 6.2 (Insightful 2000).

RESULTS

Greenhouse experiment

According to MANOVA analyses, *Castilleja levisecta* greenhouse performance differed among host treatments (Wilkes = 0.84, $F_{3,116} = 2.37$, $P = 0.014$) as well as source populations (Wilkes = 0.55, $F_{1,116} = 31.47$, $P < 0.001$), but no differences were observed among maternal lines (Wilkes = 0.42, $F_{32,116} = 1.19$, $P = 0.13$). Host treatment effects were consistent among *C. levisecta* individuals from the two source populations used in this study, as the interaction between source population and host treatment was not significant (Wilkes = 0.93, $F_{3,116} = 0.92$, $P = 0.51$). While *C. levisecta* stem number and total stem length differed among host treatments, the number of flowers did not (Table 1). Univariate ANOVA statistics for the three response variables are presented in Table 1. Post-hoc pair wise comparisons of univariate ANOVAs revealed that individuals grown with mixed hosts had a greater number of stems and total stem length compared to those grown with *F. roemeri*, but did not differ from those grown without a host or with *E. lanatum*.

Field experiment

Field survival of *C. levisecta* differed among host treatments ($DEV_{3,81} = 44.65$, $P < 0.001$), but neither source population ($DEV_{1,81} = 0.089$, $P = 0.77$) nor maternal line ($DEV_{32,81} = 34.43$, $P = 0.40$) accounted for a significant portion of the residual deviance. A higher proportion of no-host *C. levisecta* individuals survived compared to those planted with either *E. lanatum* or mixed hosts, but did not differ from plants with *F. roemeri* hosts (Fig. 1). Also, *C. levisecta* planted with *F. roemeri* hosts had significantly higher survival than those planted with *E. lanatum* (Fig. 1).

Rodent tunnel presence near transplant root crowns differed significantly among host treatments ($DEV_{3,114} = 50.17$, $P < 0.001$). *Castilleja levisecta* individuals planted with *F. roemeri* or without a host had fewer rodent holes near their root crowns compared to those planted with either *E. lanatum* or mixed hosts (Fig. 1). In addition, we measured a strong inverse relationship between *C. levisecta* survival and the presence of tunneling within the vicinity of the root crown ($F_{1,2} = 23.07$, $P = 0.04$, $R^2 = 0.92$) (Fig. 2). The odds of a *C. levisecta* transplant surviving in the field when planted without an *E. lanatum* host were 11.25 (95% C.I. = 4.29, 28.78) times greater than when co-planted with an *E. lanatum* host.

DISCUSSION

We did not find support for the complimentary diet hypothesis, which predicts that individuals with multiple nutritional sources will perform

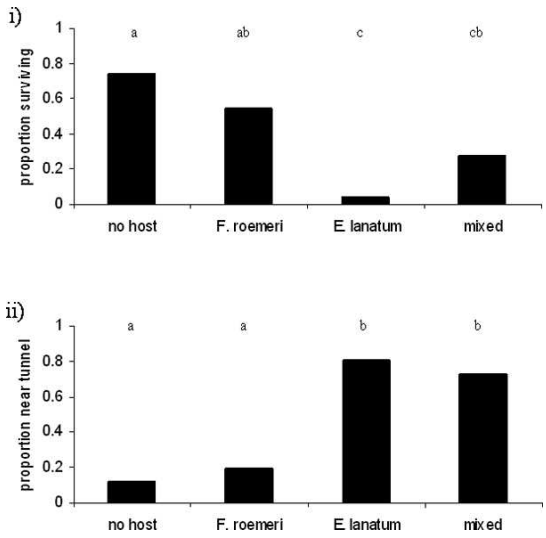

FIG. 1. i) *Castilleja levisecta* field survival by host treatment. ii) Proportion of *C. levisecta* transplants located within 15 cm of rodent tunnels. Host treatments not sharing a common letter were significantly different ($P \leq 0.05$) after Dunn-Sidak corrections.

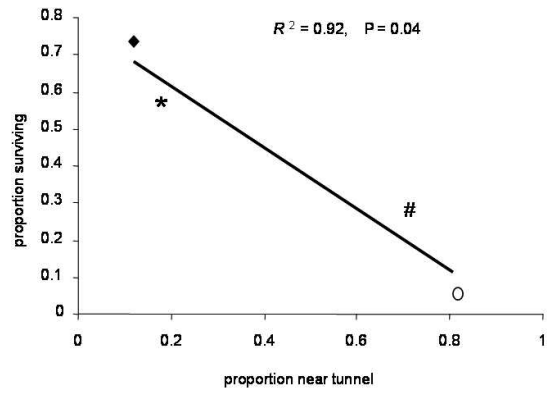

FIG. 2. Scatterplot and trendline from linear regression of the average proportion of *C. levisecta* transplants within 15 cm of a vole tunnel and average transplant survival for each host treatment (no host = ♦, *F. roemeri* = *, mixed = #, *E. lanatum* = ○).

better than those provided with a limited diet. Mixed hosts improved some measures (i.e., stem number and total stem length) of *C. levisecta* greenhouse performance compared to those paired with *F. roemeri*, but did not confer an advantage over no-host or *E. lanatum* treatments. Likewise, mixed hosts did not promote *C. levisecta* field survival. In fact, no-host controls had greater field survival than both mixed and *E. lanatum* treatments (Fig. 1). The complementary diet hypothesis may not be the most appropriate theory to apply to hemiparasite nutrition, as this hypothesis has primarily been tested in animal systems. Other studies addressing hemiparasite fitness using multiple hosts have also found mixed results. During greenhouse studies, *Melampyrum arvense* did not benefit from mixed hosts (a legume and a grass) (Matthies 1996), though *Castilleja wightii* growth and reproductive output were improved by simultaneous attachment to two host species (a legume and an aster) (Marvier 1998a). However, greenhouse studies may oversimplify field dynamics and should be extrapolated to the field with caution. For example, we observed strong indirect effects of herbivory mediated by host species in the field, which has important consequences for *C. levisecta* recovery efforts.

While we observed improved *C. levisecta* stem performance when grown with mixed hosts relative to *F. roemeri* in the greenhouse, the number of flowers produced did not differ among host treatments. Mixed hosts may have improved *C. levisecta* nutrition by providing complimentary resources, thereby improving stem growth relative to *F. roemeri* hosts. Alternatively, root competition may explain why *F. roemeri* is a poor host in pots, as pots with *F. roemeri* were generally more root bound than other host treatments (Beth Lawrence, pers. obs.). This is consistent with our previous work that found *C. levisecta* grown in pots with *F. roemeri* were smaller and flowered less frequently in the second growing season compared to those potted with *E. lanatum* (Kaye 2001). This explanation is more plausible, as *C. levisecta* performed similarly among all other treatments, but did poorly when paired just with *F. roemeri*. Our greenhouse results may also have been confounded by our judicious use of fertilizer, as attachment to hosts may not confer fitness benefits in the presence of abundant nutrients.

Vole activity had strong indirect effects on *C. levisecta* field survival mediated by host species. Populations of the grey-tailed vole (*Microtus canicaudus*) were larger than average in the Willamette Valley during the 2005 field season due to a mild winter in 2004–05, increasing herbivore pressure on *C. levisecta* transplants and impacting the region's grass seed crop. Nine Oregon counties were declared agricultural disaster areas by the U.S. Department of Agriculture due to large crop losses from voles (A.P. 2005). Although population sizes in 2005 were atypically large, voles are ubiquitous in Pacific Northwest prairies and are major herbivores contributing to grassland dynamics (Wilson and Carey 2001). Further, global warming may increase the frequency of mild winters in the Pacific Northwest (Leung and Ghan 1999) and result in greater regularity of vole outbreaks. Selective herbivory by voles in other grassland systems has been shown to dramatically alter species composition and diversity (Batzli and Pitelka 1970; Howe and Lane 2004). Using exclusion experiments, Howe

and Lane (2004) observed that meadow voles eliminated otherwise common plants due to preferential herbivory.

Castilleja levisecta field survival also did not support the complimentary diet hypothesis, possibly as a result of indirect effects from herbivore activity. While herbivory was evident on all surviving *C. levisecta* individuals at the study site, vole tunneling and field mortality were strongly associated with host treatments that included *E. lanatum*, whose roots may have been particularly palatable to voles. *Castilleja levisecta* plants paired with two *E. lanatum* individuals had higher field mortality than those planted with a single *E. lanatum* individual (mixed host), although these effects were not strictly additive (Fig. 1). The mechanism contributing to high mortality of *C. levisecta* individuals associated with *E. lanatum* is unclear, but root system disturbance, direct grazing of *C. levisecta* roots, or the indirect effect of reduced host vigor/survival likely contributed to this observation. Meanwhile, *C. levisecta* individuals planted without a host or with *F. roemeri* had much higher survival rates and less rodent tunneling. This indicates that voles did not just target potting soil or areas with low root density to tunnel in, but were specifically attracted to *E. lanatum*. Foliage and roots of plants in the genus *Eriophyllum* contain sesquiterpene lactones (Bohlmann et al. 1981), an extremely diverse group of compounds that may be desirable to herbivores due to anti-fungal, anti-bacterial, anti-tumourgenic, or anti-inflammatory properties (Picman 1986), and may have contributed to increased vole tunneling in the vicinity of *E. lanatum*.

Although we have provided evidence that vole activity mediated *C. levisecta* survival through host species in the field (Fig. 2), an alternative process could be responsible for the observed field patterns. Due to a malfunction of the automatic watering system, we observed differential survival of the potted plants during the 2004 summer in the shadehouse. Survival was greater among no-host (100%) and *F. roemeri* (79.5%), than among *E. lanatum* (66.7%) and mixed hosts (54.4%), similar to the pattern of differential survival we observed in the field. Thus it is possible that our field survival rates were only spuriously correlated with vole activity and that survival of *C. levisecta* is directly influenced by host treatment, rather than indirectly via herbivore activity.

Results from our greenhouse and field studies suggest that planting *C. levisecta* with a host may not be absolutely necessary, but may confer some advantages to field plantings. Although our findings are likely context dependent, no-host controls performed as well or better than all other host treatments in both greenhouse and field environments. Host plants can provide water and nutrients to hemi-parasites during periods of critical environmental stress (Kuijt 1969; Press 1989). However, under horticultural growing conditions with ample water, nutrients, and light, *C. levisecta* individuals produced abundant biomass and had high reproductive output without hosts. In our field study, no-host *C. levisecta* individuals had the highest proportion surviving ($\bar{x} = 0.78$), although at the time of monitoring these plants had yet to experience summer drought conditions typical of the region. Natural populations of *C. levisecta* emerge in early March, flower in May, and senesce in July in response to dry conditions (Caplow 2004).

Summer drought is a strong selective force resulting in substantial *C. levisecta* transplant mortality, as field survival is typically high the first growing season, but is generally reduced the second growing season (Lawrence 2005; Pearson and Dunwiddie 2006; Swenerton 2003; Wayne 2004). Results from a companion common garden experiment indicate that planting a perennial host with *C. levisecta* transplants improves second year survival (Lawrence 2005). Second year survival at a site where individuals were planted with *F. roemeri* was particularly high ($\bar{x} = 0.75$), compared to the average proportion surviving at the other nine common gardens ($\bar{x} = 0.21$), that were not provided a host. Pearson and Dunwiddie (2006) observed greater *C. levisecta* flower production when grown with *E. lanatum* compared with *F. roemeri*, but field survival was greater with *F. roemeri*. Another field experiment also observed greater *C. levisecta* survival when outplanted with *F. roemeri* relative to no-host and *E. lanatum* treatments (S. Reichard 2005, University of Washington, pers. comm.). *Castilleja hispida* Benth., which can hybridize with *C. levisecta*, also had higher field survival when planted with *F. roemeri* than when planted with no host (Schmidt 1998). These observations suggest that planting a perennial host with *C. levisecta* in the field is beneficial, and may allow the parasite to take advantage of host roots to exploit nutrients and water from a larger volume of soil during periods of environmental stress. Further, this suggests that *C. levisecta* survival is higher when planted with *F. roemeri* than *E. lanatum*, and this may be due, at least in part, to preferential vole herbivory of *E. lanatum*.

Other native perennial species, including legumes and showy angiosperms that can attract pollinators, may also be appropriate hosts for *C. levisecta*. Leguminous hosts are commonly better hemiparasite hosts than grass species because of their capacity to fix nitrogen (Adler 2003; Gibson and Watkinson 1991; Matthies 1997; Seel and Press 1993). Additionally, alkaloid uptake from leguminous hosts can confer resistance to herbivory (Adler 2002), and increase pollinator visitation (Adler et al. 2001). Although the mycorrhizal

status of *C. levisecta* has not been investigated, many hemiparasites in the Orobanchaceae are considered non-mycorrhizal (Harley and Harley 1987). The mycorrhizal status of the host plant however, can influence the performance of the hemiparasite. Studies have shown that hemiparasites attached to mycorrhizal hosts have greater biomass and flower production than those growing with non-mycorrhizal hosts (Davies and Graves 1998; Salonen et al. 2001). We suggest that new *C. levisecta* potential host species and mycorrhizal inoculation of hosts should be examined experimentally in the field to further examine the complimentary diet hypothesis and improve the success of large-scale reintroductions of this endangered species.

Implications for practice

- Conservation decisions should be based on experimental research conducted under conditions similar to those of the intended application; *C. levisecta* greenhouse performance was a poor predictor of field survival. Extrapolation of greenhouse results to natural systems can oversimplify the complex biotic interactions that species are exposed to in the field, and worse, suggest inappropriate management actions.
- Greenhouse propagation of endangered hemiparasites like *C. levisecta* may not require a host, but growth and survival after field planting may be improved by planting with additional species. See (Lawrence and Kaye 2005) for details on propagation techniques for *C. levisecta*.
- Failure to find support for the complimentary diet hypothesis with *C. levisecta* suggests that outplanting rare hemi-parasites with multiple hosts may not be necessary.
- We recommend against planting hemiparasites with hosts that are attractive to herbivores when and where these animals are present. We suspect planting *C. levisecta* with a perennial host will increase future field performance and recommend using *F. roemeri* over *E. lanatum* as a host for *C. levisecta* recovery efforts.
- Herbivore management should be an integral part of rare hemiparasite recovery and management. Herbivore control may involve the same actions as prairie habitat management, such as mowing or burning to reduce the accumulation of thatch. Large fences can be erected to exclude ungulate browsers from an outplanting, while small wire cages dug into the ground can prevent rodent grazing of individual plants.

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