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

THESIS CHAPTER 4

Direct and indirect effects of host plants: Implications for reintroduction of an
endangered hemiparasitic plant (*Castilleja levisecta*)

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Chapter 4: Direct and indirect effects of host plants: Implications for reintroduction of an endangered hemiparasitic plant (*Castilleja levisecta*)

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 *Castilleja levisecta* (Scrophulariaceae), a rare hemiparasite, was affected by the availability of different host combinations in the greenhouse and in the field. *Castilleja levisecta* individuals were grown with two grass individuals (*Festuca roemeri*; Poaceae), two non-grass individuals (*Eriophyllum lanatum*; Asteraceae), one individual of each of these species, or without a host. Our greenhouse results provide little support for the complimentary diet hypothesis, which states that parasites grown with multiple host species perform better than individuals grown alone or with a single host. *Castilleja levisecta* individuals grown with two different species performed better than those co-planted only 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*. Field survival was significantly higher among no-host *C. levisecta* individuals than those grown with *E. lanatum* or mixed host treatments.

Our results emphasize the importance of basing conservation decisions on experimental research conducted under conditions similar to those of the intended application. Our greenhouse results were a poor predictor of field performance. Increases of *C. levisecta* seed are possible in a horticultural setting with any of the host treatments we tested if adequate water and nutrients are supplied. However, we do not suggest co-planting *C. levisecta* with *E. lanatum* in the field. Although no-host *C. levisecta* individuals had the greatest first year field survival, we suspect that perennial host plants will be beneficial to future survival. Therefore, we recommend planting *C. levisecta* in the Willamette Valley, OR with *F. roemeri*.

INTRODUCTION

Parasitic plants are an important component of many plant communities because they are capable of altering productivity (Marvier 1998b; Matthies 1997), competitive

interactions (Gibson & Watkinson 1991; Matthies 1996), and community structure (Gibson & Watkinson 1992; Press 1998). Although many parasitic plants are considered agricultural pests, some are of conservation concern (Marvier & Smith 1997). Rare parasitic species pose an interesting challenge to restoration practitioners. In addition to the diversity of obstacles during typical reintroductions, rare parasites may also be limited by their host requirements. Uncertainties associated with the availability and quality of hosts at restoration sites, as well as parasite host specificity, are likely to impede recovery of parasitic plants (Marvier & Smith 1997). Successful management of rare parasites necessitates consideration of their unique biology. We conducted greenhouse and field experiments with *Castilleja levisecta*, a hemiparasite endemic to the prairies of the Pacific Northwest, to evaluate its host preferences and support recovery actions in the southern portion of its' historic range.

Although facultative hemiparasites are photosynthetic and do not require a host plant, they often form haustoria, or physical connections, with other root systems to obtain nutrients, water, and secondary compounds from their host (Kuijt 1969; Press 1989). In natural systems, unattached mature facultative parasites are rare, and attachment to a host generally stimulates the parasite's growth (Kuijt 1969). Most members of the genus *Castilleja* are considered generalist hemiparasites, capable of parasitizing multiple host species (Dobbins & Kuijt 1973; Heckard 1962). However, the degree to which a host stimulates hemiparasite fitness varies considerably among host species (Chuang & Heckard 1971; Gibson & Watkinson 1992; Marvier 1998b; Matthies 1996, 1997; Seel & Press 1993). Interactions between plant parasites and host species can have direct and indirect effects on both host and parasite performance, as well as their pollinators (Adler et al. 2001) and herbivores (Adler 2002; Adler 2003; Adler et al. 2001; Marko 1996; Marvier 1996). For example, parasitic plants can acquire secondary compounds from host species (Govier et al. 1967; Schneider & Stermitz 1990; Stermitz & Harris 1987), which in turn can alter species interactions. 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 & Watkinson 1989; Matthies 1996). The complimentary diet hypothesis

proposes that generalist consumers perform better on a mixed diet relative to a homogenous diet, due to improved nutrient balance and/or dilution of toxic secondary plant compounds (Bernays et al. 1994). Many taxa benefit from multiple food sources, including insects (Bernays et al. 1994), gastropods (Pennings et al. 1993), reptiles (Bjorndal 1991), and hemiparasitic plants (Marvier 1998a). Therefore, we believe that providing multiple host species for rare parasites may increase fitness components compared to single or no-host plantings and facilitate recovery.

Castilleja levisecta is a federally listed hemiparasite currently restricted to eleven sites in the Pacific Northwest and extinct in the southern portion of its historic range including the Willamette Valley, Oregon. Recovery criteria for *C. levisecta* call for the existence of twenty populations composed of 1,000 flowering individuals (U.S.F.W.S. 2000). However, the species has limited capacity for natural dispersal and colonization of new sites, necessitating *ex situ* conservation techniques to meet recovery goals. A strategic reintroduction plan has been prepared to support the long-term viability of *C. levisecta* and calls for the establishment of new populations within its historic range (Caplow 2004). Although several studies have investigated *C. levisecta* host use, clarification of its host requirements 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 co-planting *C. levisecta* in the field with a perennial host increases reproductive output (Wayne 2004), and possibly survival rates (B. Lawrence personal observation). Greenhouse observations indicate that *C. levisecta* can form haustorial connections with several perennial prairie species (e.g., *Leucanthemum vulgare*, *Eriophyllum lanatum*, *Festuca roemerii*, and *Fragaria vesca*), and with itself when grown alone (Kaye 2001; Wentworth 2001). Field experiments indicate that outplanting *C. levisecta* with *F. roemerii* increases the number of inflorescences produced compared to no-host controls, although host presence did not effect field survival rates (Wayne 2004). In addition, the species is frequently eaten by small mammals (Caplow 2004; Wayne 2004), but we are not aware of any previous evaluations of host-mediated effects of herbivory on *C. levisecta*.

Here, we present theoretical and practical explorations of *C. levisecta* host use during greenhouse and field studies in the Willamette Valley, OR. We test the hypothesis that *C. levisecta* individuals grown with multiple host species perform better than individuals grown alone, or with a single host species, and that host-interactions affect herbivory under field conditions. We compare our greenhouse and field results and provide recommendations for future *C. levisecta* recovery efforts.

METHODS

Study species

Castilleja levisecta (Orobanchaceae) is a short-lived (5-6 years), multi-stemmed, perennial endemic to the native grasslands of the Western Pacific Northwest. It is an out-crossing species primarily pollinated by *Bombus* spp. and is known only to reproduce by seed (Kaye & Lawrence 2003; Wentworth 2001). The eleven remaining *C. levisecta* populations are concentrated in the San Juan Islands of the Puget Trough eco-region, and are found on sandy, well drained soils of glacial origin (Chappell & Caplow 2004). Only one inland prairie population remains in Thurston County, WA, while the ten island populations are generally located on south-west facing coastal prairies that are dominated by graminoids and forbs (Chappell & Caplow 2004). Despite the species' rarity, its remaining populations maintain unusually high levels of genetic diversity compared with other endemic species and even other members of the figwort family (Godt et al. 2005).

Castilleja levisecta was last collected in the Willamette Valley, OR in 1938 (Gamon 1995). All that remains of the historic populations of this region are herbarium records, which do not describe the specific location or habitat of these populations. Based on information from herbarium specimens and site visits, we believe that *C. levisecta* once inhabited upland prairies in the Willamette Valley. These grass dominated systems are often associated with *Quercus garryana*-savanna that occur on well-drained soils commonly found on the valley foothills (Franklin & Dyrness 1988). The unglaciated soils of these foothills are dominated by clay and silt from weathering basalt and are generally well-drained.

Greenhouse experiment

To test for differences in *C. levisecta* performance in different host combinations, we randomly assigned individuals to one of four host treatments, including no-host (control), two *E. lanatum* individuals, two *F. roemeri* individuals, or one individual of each of these host species (“mixed hosts”). We used plant material from two *C. levisecta* source populations, Ebey’s Landing and Forbe’s Point, located on Whidbey Island, WA. Twenty host treatment replicates were conducted for each source population, for a total of 40 replicates per host treatment (n= 160). *Eriophyllum lanatum* and *F. roemeri* were used as host plants because *C. levisecta* forms haustorial connections with them (Wayne 2004, B. Lawrence pers. obs.). Additionally, these species are native perennials common to the prairies of the Pacific Northwest and are likely to be present at reintroduction sites.

Castilleja levisecta seed capsules were collected from source populations in August 2003 to provide seeds for this experiment. Seeds were moist-cold stratified on filter paper for six weeks at 5 °C, then transferred to a warm room for one week with light and temperature on a 12 hour cycle (15 °C/25 °C). On 1 December 2003, germinants were planted into cell flats in a well-drained medium (Sunshine Mix #4 Aggregate Plus) amended with slow release micro- and macro- nutrients. Plants were grown in a greenhouse with 400 watt high pressure sodium lights and temperature fluctuating every 12 hours (12 °C/18 °C).

Host treatments were randomly assigned on 28 January 2004 and were transplanted into gallon pots. *Castilleja levisecta* individuals and potential hosts were planted in a triangle with all plants 10 cm apart (Figure 4-1); *C. levisecta* individuals assigned the no-host treatment were planted in the center of the pot. *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 a year old when paired with *C. levisecta*. We attempted to equalize above- and below-ground biomass among provided hosts. Plants were randomized on greenhouse benches and fertilized biweekly with a liquid 15-30-15 fertilizer. Plants were moved to a shade-house in June 2004 and received supplemental water throughout the summer. We recorded the total stem length, stem number, and flower number on each *C. levisecta* individual on 10 May 2004, approximately 15 weeks after potting the parasites and hosts together.

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 study site was located at Pigeon Butte, Finley National Wildlife Refuge, OR, 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 invasive non-native pasture grasses (e.g., *Festuca arundinacea* and *Arrenatherum elatius*). Pigeon Butte is situated on the shoulder of a butte at 150 m elevation and is dominated by Typic Argixerolls of the Dixonville series that are well-drained, silty-clay-loam soils, formed from weathered basalt. Average annual precipitation 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 into square meters within a 10m x 15m grid. A balanced design could not be executed in the field because many of the greenhouse plants died during a malfunction of the automatic watering system in summer 2004. However, at least 22 replicates of each of the four host treatments were transplanted into the field (n= 121). *Castilleja levisecta* individuals at the time of outplanting were mostly dormant, with little above-ground biomass.

Field transplants were monitored on 23 May 2005. Vole abundance was unusually high in the Willamette Valley, OR during the 2005 growing season. All surviving *C. levisecta* individuals at Pigeon Butte were subjected to some herbivory, most likely from grey-tailed voles (*Microtus canicaudus*). Stem length and number were not reliable measures of *C. levisecta* performance, as herbivory appeared to stimulate resprouting and alter plant morphology (B. Lawrence, pers. obs.) Therefore, we measured *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 we measured herbivore pressure by voles as presence or absence of their tunnels within 15cm of the transplant root crown.

Statistical analyses

Because our measures of plant size and fitness (stem length, stem and flower number) were correlated with one another, we combined them into a single index of plant performance for each greenhouse plant using Principal Components Analysis (PCA) in PC-ORD v.4.25 (McCune & Mefford 1999). The objective of PCA is to find the strongest linear correlation structure among variables and reduce them to a smaller number of synthetic variables that represent the most information in the original data set (McCune & Grace 2002). Prior to PCA, total stem length and stem number were log transformed to improve homoscedasticity.

PCA scores from axis 1 were used as the response variable in analysis of variance (ANOVA) to determine if performance differed among host treatments in the greenhouse. 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 *C. levisecta* (Kaye 2001). This and all further data analyses were conducted in S-PLUS v. 6.2 (Insightful 2000). The significance of all pair-wise host treatment comparisons were tested using Dunn-Sidak corrections.

We tested for differences in *C. levisecta* field survival and vole tunnel presence among host treatments using binary logistic regression analyses. We used drop in deviance tests with a chi-square distribution to test for significance. Dunn-Sidak corrections were used to correct for multiple pair-wise comparisons between host treatments. We tested the linear relationship between vole tunnel presence and plant survival by host treatment using linear regression. Finally, we calculated an odds ratio to compare the odds of *C. levisecta* survival when co-planted with *E. lanatum* vs. the odds of survival when not planted with this species.

RESULTS

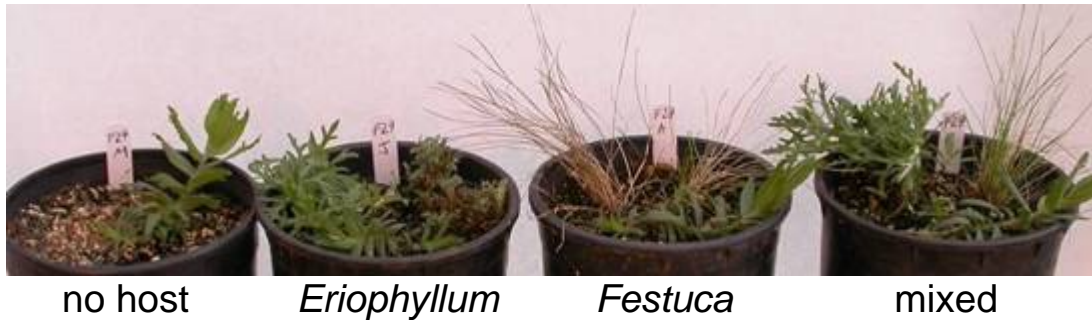


Figure 0-1. Host treatments one week after potting *C. levisecta* and hosts together.

Greenhouse experiment

The first PCA component accounted for 59.9% of the variation in stem length, stem number, and flower number. Comparison of eigenvalues to those produced by a random model indicated that only the first axis contained more information than expected by chance ($p= 0.020$), supporting our decision to use scores from this axis in further analyses. The solution was rotated to align stem length with axis 1 (Figure 4-2), because this axis was most highly correlated stem length ($r^2= 0.93$). Axis 1 also accounted for substantial variation in flower and stem number ($r^2= 0.50, 0.38$, respectively). Axis 2 is primarily a function of flower and stem number ($r^2= 0.46, 0.59$, respectively). Large, flowering plants are located in the upper right-hand region of the ordination space, while small, non-reproductive plants with few stems are located in the lower-left portion of the ordination. The component loadings (eigenvectors) for the first principal component are: stem length (0.718), stem number (0.457), and flower number (0.526). The average performance measures associated with PCA scores for each host treatment are presented in Table 4-1.

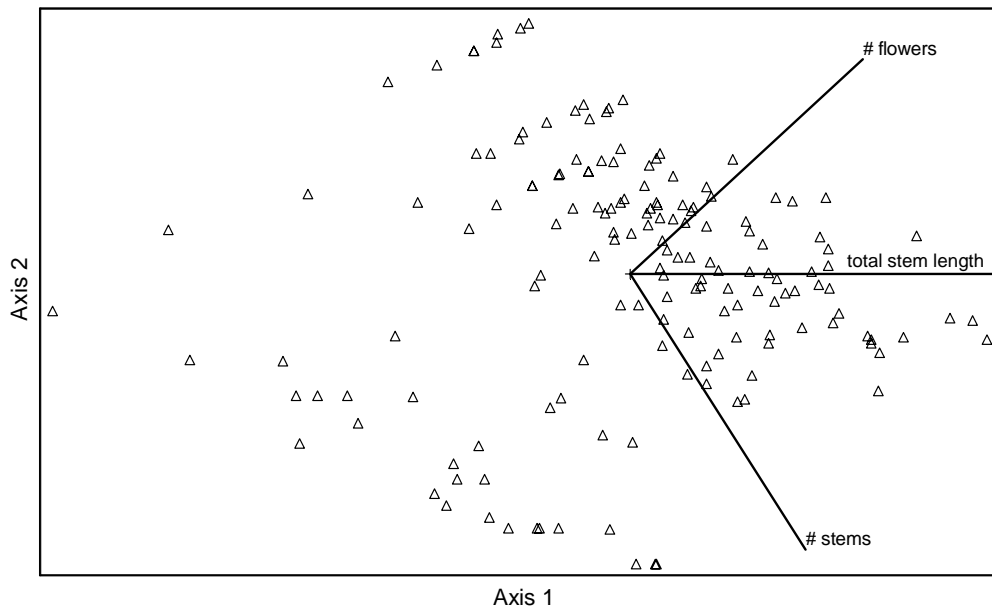


Figure 0-2. Plot of the first two principal components for 159 greenhouse grown *C. levisecta* individuals based on three measurements of performance. Each point represents a *C. levisecta* individual. Vector overlays of the performance measures depict the strength and direction of correlation with the two axes.

Table 0-1. Mean (± 1 SE) *C. levisecta* composite performance (PCA) scores and stem length, flower number and stem number for plants grown in the greenhouse under each host treatment.

host treatment	PCA score	stem length (cm)	# flowers	# stems
<i>F. roemerii</i>	-0.52 \pm 0.14	63.7 \pm 4.4	29.4 \pm 3.3	5.33 \pm 0.51
no host	0.07 \pm 0.20	80.7 \pm 6.4	36.9 \pm 4.5	7.24 \pm 0.60
<i>E. lanatum</i>	0.13 \pm 0.22	89.0 \pm 8.1	34.5 \pm 3.8	7.03 \pm 0.81
mixed	0.32 \pm 0.30	92.6 \pm 10.4	36.7 \pm 5.2	7.88 \pm 0.77

Castilleja levisecta performance differed significantly among host treatments in the greenhouse ($F_{3, 122} = 3.22, p = 0.025$) (Figure 4-3). Performance differed among maternal lines ($F_{32, 122} = 2.03, p = 0.003$), but overall, *C. levisecta* individuals from the two source populations performed similarly ($F_{1, 122} = 0.013, p = 0.91$). *Castilleja levisecta* individuals grown with mixed hosts were significantly larger on average than those grown with *F. roemerii*, but did not differ from those grown without a host or with *E. lanatum* (Figure 4-3).

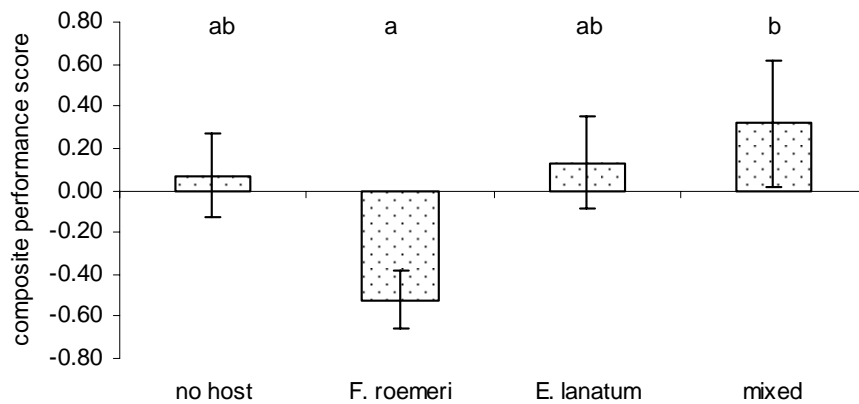


Figure 0-3. *Castilleja levisecta* greenhouse performance differed among host treatments (± 1 SE). Host treatments not sharing a common letter were significantly different ($p \leq 0.05$) after Dunn-Sidak corrections.

Field experiment

Field survival of *C. levisecta* differed significantly among host treatments ($DEV_{3, 83} = 44.65, p < 0.001$), which accounted for 26.8% of the residual deviance in the model. Neither source population ($DEV_{1, 83} = 0.089, p = 0.77$) nor maternal line ($DEV_{32, 83} = 34.43, p = 0.40$) accounted for significant residual deviance. No-host *C. levisecta* individuals survived significantly more often than those planted with either *E. lanatum* or mixed hosts, but their survival did not differ from plants with *F. roemerii* hosts (Figure 4-4). Also, *C. levisecta* planted with *F. roemerii* hosts had significantly higher survival than those planted with *E. lanatum*.

The presence of rodent tunnels near host transplants was significantly different among host treatments ($DEV_{3, 117} = 50.17, p = 0.40$). *Castilleja levisecta* individuals co-planted with *F. roemerii* or without a host had significantly fewer rodent holes near their root crowns compared to those planted with either *E. lanatum* or mixed hosts (Figure 4-5). In addition, we measured a strong inverse relationship between *C. levisecta* survival and the presence of tunneling within the vicinity of the root crown ($F_{1,2} = 23.07, p = 0.04, R^2 = 0.92$) (Figure 4-6). The odds of a *C. levisecta* transplant surviving in the field when planted without an *E. lanatum* host was 11.25 (95% C.I. = 4.29, 28.78) times greater than when co-planted with an *E. lanatum* host.

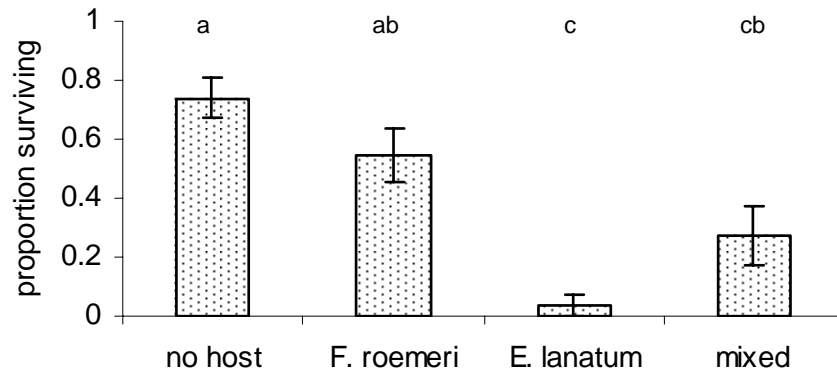


Figure 0-4. *Castilleja levisecta* field survival by host treatment (± 1 SE). Host treatments not sharing a common letter were significantly different ($p \leq 0.05$) after Dunn-Sidak corrections.

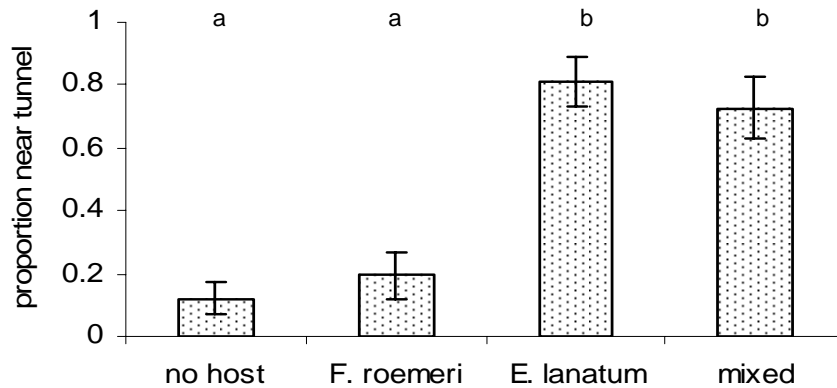


Figure 0-5. Proportion of *C. levisecta* transplants located within 15cm of rodent tunnels (± 1 SE). Host treatments not sharing a common letter were significantly different ($p \leq 0.05$) after Dunn-Sidak corrections.

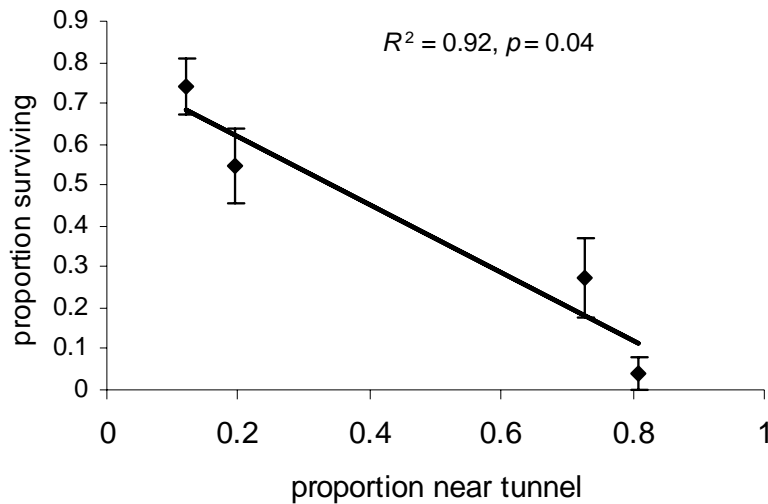


Figure 0-6. Scatterplot and trendline of the average proportion of *C. levisecta* transplants within 15 cm of a vole tunnel and average transplant survival for each host treatment.

DISCUSSION

Our results provide little support for the complimentary diet hypothesis that predicts individuals with multiple nutritional sources will perform better than those set on a limited diet. In fact, no-host controls performed as well or better than *C. levisecta* individuals co-planted with multiple host species in both greenhouse and field environments. Multiple host species may provide complimentary resources for *C. levisecta* individuals by improving nutrient balance or possibly diluting any harmful secondary compounds obtained from either host. However, the mechanism responsible for improved *C. levisecta* greenhouse performance when grown with mixed hosts compared with *F. roemerii* is unclear. Marvier (1998a) observed that half of the *C. wightii* individuals grown with mixed hosts failed to establish functional connections with one of the host species. We did not look for haustoria between *C. levisecta* and associated hosts or conduct chemical analyses of plant tissues, because such destructive sampling would have precluded our field study. We believe our greenhouse observation that *F. roemerii* is a poor host in pots may be explained by root competition: *F. roemerii* host treatment replicates were generally more root bound than other host treatments (B. Lawrence, pers. obs.). This is consistent with our previous work that found *C. levisecta*

grown in pots were smaller and flowered less frequently in the second growing season when potted with *F. roemerii* than with *E. lanatum* (Kaye 2001).

Castilleja levisecta survival in the field did not support the complimentary diet hypothesis as the mixed host treatment was indirectly and negatively affected by herbivore activity.

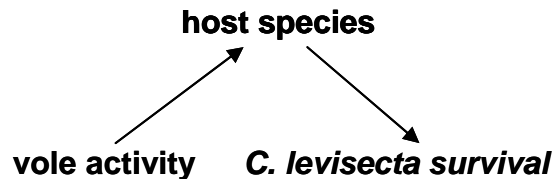


Figure 0-7. Schematic of the indirect effect of vole activity on *C. levisecta* survival mediated by host species.

Vole activity had strong indirect effects on *C. levisecta* field survival mediated through host species (Figure 4-7). Populations of the grey-tailed vole (*Microtus canicaudus*) exploded 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 devastating the region's grass seed crop. In fact, nine Oregon counties were declared agricultural disaster areas by the U.S. Department of Agriculture due to large crop losses (A.P. 2005). While herbivory was evident on all surviving *C. levisecta* individuals at Pigeon Butte, vole tunneling and field mortality were strongly associated with host treatments that included *E. lanatum*, whose roots appear to be particularly palatable to voles. *C. levisecta* plants co-planted with two *E. lanatum* individuals had higher mortality and were associated with greater tunneling activity than those co-planted with a single *E. lanatum* individual (mixed host), although these effects were not strictly additive. 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, no-host *C. levisecta* individuals and those planted with *F. roemerii* generally had much higher survival rates and less rodent tunneling. We believe 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 the genus

Eriophyllum contain sesquiterpene lactones (Bohlmann et al. 1981), which occur in the majority of tribes in the Asteraceae family (Seaman 1982). This group of compounds is extremely diverse; some act as toxins and feeding deterrents to a variety of invertebrate and vertebrate species, while others exhibit anti-fungal, anti-bacterial, anti-tumourgenic, or anti-inflammatory properties and may be desirable to herbivores (Picman 1986). The chemical attributes of *E. lanatum* likely contributed to increased vole tunneling in its' vicinity.

Results from our greenhouse and field studies suggest that co-planting *C. levisecta* with a host may not be necessary. Although our findings were likely context dependant, 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, given ideal growing conditions with ample water, nutrients, and light, *C. levisecta* individuals produced abundant biomass and had high reproductive output without host plants. In our field study, no-hosts *C. levisecta* individuals had the highest proportion surviving ($\bar{x}=0.78 \pm 0.07$). However, at the time of monitoring in 2005, these plants had yet to experience summer drought conditions typical of the Pacific Northwest. Natural populations of *C. levisecta* emerge in early March and senesce in late summer in response to dry conditions (Caplow 2004). Other work suggests that summer drought is a strong selective force resulting in differential *C. levisecta* transplant mortality, as field survival is typically high the first growing season, but drops dramatically the second growing season (B. Lawrence pers. obs.; Swenerton 2003; Wayne 2004). We have some evidence that indicates co-planting a perennial host with *C. levisecta* transplants improves second year survival (Chapter 3). During common garden experiments with *C. levisecta*, transplants were not provided with a host except at a site established in an agricultural field, where individuals were co-planted with a perennial grass (*F. roemerii*). Second year survival of transplants was particularly high at this site ($\bar{x} = 0.75 \pm 0.04$), compared to the average proportion surviving at the other nine common gardens ($\bar{x} = 0.21 \pm 0.06$) or Pigeon Butte ($\bar{x} = 0.51 \pm 0.05$). This suggests that co-planting a perennial host with *C. levisecta* in the field is beneficial, and may allow the parasite to take advantage of host

roots that enable them to exploit nutrients and water from a larger volume of soil during periods of environmental stress.

Management implications

Our results emphasize the importance of basing conservation decisions on experimental research conducted under conditions similar to those of the intended application. Simple 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. Our greenhouse results suggested that *F. roemerii* was a poor host for *C. levisecta*, but our field studies showed that this species is superior to *E. lanatum* for promoting plant survival at reintroduction sites when voles were present. If we had limited our experiments to the greenhouse we could have made recommendations that would have resulted in poor *C. levisecta* field-establishment.

It may be useful to grow *C. levisecta* in pots in a horticultural setting to mass produce seeds for recovery efforts. Pollinators are essential to fruit and seed production in *C. levisecta* because the species is an obligate outcrosser (Kaye and Lawrence 2003). We observed abundant seed set in our shade-house environment where pollinators (i.e. *Bombus* spp.) were present. If seed increases of *C. levisecta* in a horticultural setting is a management objective, we recommend not using a host if plants are provided with adequate water and nutrients or co-planting with *E. lanatum*. In the field however, we do not recommend co-planting *C. levisecta* with *E. lanatum*, as this host species was associated with vole tunneling and high *C. levisecta* mortality rates. First year field survival was highest for no-host *C. levisecta* individuals and those planted with *F. roemerii*. We suspect co-planting *C. levisecta* with a perennial host will increase future field performance and recommend using *F. roemerii* as a host for Willamette Valley *C. levisecta* recovery efforts. This grass was once a dominant species of upland prairies in the region, is relatively easy to grow, and was not linked to destructive herbivore activity.

Although the 2005 field season was an anomalous year in terms of vole abundance, herbivore management, including that of deer, elk, and rabbits, will clearly be an integral part of *C. levisecta* recovery efforts. Herbivore management may actually involve the same actions as prairie habitat management (e.g., mowing or burning, fencing) and improve growing conditions for *C. levisecta*. Prescribed burns during times

of *C. levisecta* dormancy have been used to manage vole populations at extant populations (P. Dunwiddie, pers. comm.). Fire consumes litter which reduces cover and leaves voles susceptible to predation while also reducing competition for light resources. Further, mounting evidence suggests that *C. levisecta* responds favorably to fire in Washington prairie (Dunwiddie et al. 2000). Fencing may also be used to deter herbivores; two and a half meter fences effectively excluded large mammals from our common garden experiments in the Willamette Valley, while wire cages dug into the ground successfully prevented rabbit herbivory at an extant population on Whidbey Island.

Further investigation of the host dynamics of *C. levisecta* may increase our capacity to successfully reintroduce this species to the southern portion of its historic range. Although the mycorrhizal status of this species has not been investigated, many hemiparasites in the Scrophulariaceae are considered non-mycorrhizal (Harley & Harley 1987). However, the mycorrhizal status of the host plant can influence the performance of the hemiparasite. Several studies have shown that hemiparasites attached to mycorrhizal hosts have greater biomass and flower production than those growing with non-mycorrhizal hosts (Davies & Graves 1998; Salonen et al. 2001). Native perennial species other than *F. roemerii*, especially 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 & Watkinson 1991; Matthies 1997; Seel & Press 1993). Additionally, alkaloid uptake from leguminous hosts can confer hemiparasite resistance to herbivory (Adler 2002), and increase pollinator visitation (Adler et al. 2001). We suggest that mycorrhizal inoculation of *C. levisecta* host plants and new potential host species should be examined experimentally in the field to improve the success of large-scale reintroductions of this endangered species.

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