

HOST EFFECTS ON HERBIVORY AND POLLINATION IN A HEMIPARASITIC PLANT

LYNN S. ADLER¹

Center for Population Biology and Department of Entomology, University of California, Davis, California 95616 USA

Abstract. The indirect effects of hosts on interactions between parasites and other species are not well understood, and it may be difficult to predict the outcome of host species effects on parasite performance due to the complexity of potential direct and indirect effects. For example, parasitic plants obtain defensive compounds as well as nutrients from their hosts, and thus many attributes of parasitic plants are dependent on the quality of their host species. Here I measure the effect of a lupine host species (*Lupinus argenteus*) compared to other host species on herbivory, pollination, and female plant fitness in the hemiparasite Indian paintbrush (*Castilleja miniata*) using a series of field experiments. Association with lupine was determined in the field by assaying Indian paintbrush leaves for lupine alkaloids. I found that Indian paintbrush plants parasitizing lupines experienced reduced herbivory from plume moth larvae, agromyzid fly larvae, and deer, relative to Indian paintbrush plants parasitizing other host species. However, there was no correlation between alkaloid content of inflorescences and plume moth performance. Host species did not affect pollinator preference for Indian paintbrush in the field. Indian paintbrush parasitizing lupines produced twice as many seeds overall as Indian paintbrush parasitizing other host species. Correlations suggest that this benefit arises both from reduced herbivory and increased nitrogenous resources. The reduction of herbivory in Indian paintbrush plants parasitizing lupines indicates that host species can affect performance of hemiparasites via indirect pathways, and that the larger community of herbivores could alter the impact of a host on its plant parasites.

Key words: *Castilleja miniata*; hemiparasitic plants; herbivory; host–parasite interactions; Indian paintbrush; indirect effects; lupine; *Lupinus argenteus*; plant chemical defense; pollination; quinolizidine alkaloids.

INTRODUCTION

All organisms experience simultaneous, and at times conflicting, selection pressures resulting from direct and indirect interactions with their biotic environment. Indirect effects occur when the interaction between two species is modified by the presence of a third species (Miller and Travis 1996), whereas direct effects involve only two species in a pairwise interaction. Because indirect effects may occur in the same or opposite direction as direct effects, the combined outcome of multiple species interactions on a focal individual may be difficult to predict from studying only pairwise interactions in the absence of a community context (Strauss 1991, Schoener 1993, Wootton 1994).

Parasitic plants are diverse (>3000 species), are present in every major ecosystem (Kuijt 1969, Press and Graves 1995), and have strong impacts on community structure and dynamics (Pennings and Callaway 1996, Marvier 1998b). While parasites often have strong negative impacts on their hosts (e.g., Gibson and Watkinson 1991, Graves 1995, Matthies 1995, Seel and Press 1996, Silva and Martinez Del Rio 1996, Davies and

Graves 1998), different hosts can also affect their parasites by both direct and indirect pathways. Because parasitic plants acquire both nutrients (Press and Graves 1995) and defensive compounds (Arslanian et al. 1990, Boros et al. 1991, Mead et al. 1992, Stermitz and Pomeroy 1992, Stermitz et al. 1993) from their hosts, many attributes of parasitic plants are dependent on the qualities of their hosts. Thus, there is the potential for tritrophic interactions between host plants, parasitic plants, and herbivores or mutualists of the parasite, but the overall impact of a host on a parasitic plant has rarely been addressed in the context of other, interacting species.

One of the most apparent ways that host species could affect herbivores of parasitic plants is by the uptake of defensive compounds. Alkaloid uptake in one hemiparasite species, *Castilleja indivisa*, has been experimentally manipulated in the field by growing plants with high-alkaloid and low-alkaloid lines of the host *Lupinus albus* (Adler 2000a). By using lines of the same host species that varied in alkaloid production, the impact of alkaloid uptake was isolated from other effects of parasitizing different host species. *Castilleja indivisa* grown with high-alkaloid hosts had reduced herbivory, increased pollinator visits, and increased lifetime seed set compared to *C. indivisa* parasitizing low-alkaloid hosts (Adler 2000a). Path analysis dem-

¹ Current address: Department of Biology, Virginia Tech, Blacksburg, Virginia 24061 USA. E-mail: lsadler@vt.edu

onstrated that pollinators were not directly attracted to alkaloids, but rather that alkaloids, by reducing bud herbivory, increased the number of open flowers on alkaloid-containing plants and thereby increased pollinator attraction (Adler et al. 2001).

The previous study isolated the effect of one factor, alkaloid content, on herbivores, pollinators, and lifetime seed set of a parasitic plant. However, in the field, generalist parasitic plants are presented with a range of host species that vary in many aspects including defensive chemistry. Lupine species are common hosts of several parasitic plant species (Stermitz and Harris 1987, Stermitz et al. 1989, Arslanian et al. 1990, Schneider and Stermitz 1990, Boros et al. 1991, Baeumel et al. 1992, Stermitz and Pomeroy 1992, Jeschke et al. 1994, Marvier 1995, 1998a, Adler and Wink 2001), and they differ from nonleguminous hosts in their ability to fix nitrogen (via association with symbionts) as well as in their alkaloid content. The impact of lupines or other alkaloid-containing host species on herbivores of a parasitic plant has only been assessed in a handful of studies to date, each with different conclusions (Stermitz et al. 1989, Marko et al. 1995, Marvier 1995, 1998a). No study has yet considered the effect of different host species on pollinators of a parasitic plant.

The indirect effects of hosts on interactions between hemiparasites and other species are not well understood, and it may be difficult to predict the outcome of host species effects on parasite performance in a community context due to the complexity of potential direct and indirect effects. For example, the availability of nitrogen from a host species might benefit a parasite by providing greater resources for growth, defense, and/or reproduction (Chapin 1980). However, increased nitrogen might also make hemiparasites more palatable to their herbivores (Marvier 1995, Kytö et al. 1996) and thus be detrimental to hemiparasite fitness. Similarly, secondary compounds might benefit a hemiparasite by increasing resistance to herbivory, which might also make plants more attractive to pollinators (Adler 2000a, Adler and Wink 2001). However, these compounds may also be detrimental if they are damaging to the hemiparasite (McKey 1974, Chew and Rodman 1979, Fowden and Lea 1979) or deter mutualists such as pollinators (Strauss et al. 1999).

Castilleja miniata, or Indian paintbrush, is a generalist hemiparasite that parasitizes many host species, including the native lupine *Lupinus argenteus*. Indian paintbrush individuals obtain quinolizidine alkaloids when parasitizing several species of lupines, but not when parasitizing other host species (McCoy and Stermitz 1983, Stermitz et al. 1986, Stermitz and Harris 1987, Adler and Wink 2001). To determine the effect of different host species on Indian paintbrush performance and on the interactions between Indian paintbrush and its herbivores and pollinators, field observations and experiments were conducted over a three-

year period at the Rocky Mountain Biological Laboratory in Colorado, USA. Specifically, I addressed the following questions:

1) How is damage by the principal herbivores of Indian paintbrush affected by parasitizing a lupine, compared to other host species?

2) Is herbivore performance correlated with alkaloid content of Indian paintbrush?

3) How is pollinator visitation in Indian paintbrush affected by parasitizing a lupine host, compared to other host species?

4) How is Indian paintbrush performance (biomass, seed production, seed mass, and nitrogen content) affected by parasitizing a lupine host, compared to other host species?

Taken together, these studies quantify the net impact of lupine hosts on a plant parasite and investigate the importance of indirect effects of host species on a parasitic plant via changes in herbivory and pollination.

METHODS

Study system

Castilleja miniata Douglas (Scrophulariaceae; Indian paintbrush), and *Lupinus argenteus* Pursh (Fabaceae; lupine) are long-lived perennials that grow abundantly at Emerald Lake (Gunnison County, Colorado, USA; elevation 3000–3300 m), ~10 km from the Rocky Mountain Biological Laboratory (RMBL). The major habitat of *C. miniata* is subalpine meadows surrounded by subalpine fir forest; the dominant vegetation in these meadows is grasses and perennial forbs. The growing season is July–August. Three sites were chosen based on accessibility and the abundance of Indian paintbrush (≥ 75 individuals/site). Sites were ≥ 200 m in diameter and in discrete meadows within 500 m of each other, separated by wide stands of fir trees. Sites 1 and 2 were adjacent (elevation 3336 m, above the high road on the east slope; site 1 at 39°00'42" N, 107°02'29" W; site 2 at 39°00'44" N, 107°02'32" W); site 1 was open, and site 2 was more shaded. Site 3 was lower, sunny, and moister due to a small adjacent stream (3150 m, between the low and high roads on east slope; 39°00'41" N; 107°02'32" W). Voucher specimens of *C. miniata* and *L. argenteus* from each site have been deposited at the RMBL Herbarium. The major potential host species in order of relative abundance were: (site 1) various grasses (including *Bromus carinatus*, *Dactylis glomerata*, *Deschampsia cespitosa*, *Elymus trachycaulus*, *Festuca thurberi*, *Koeleria macrantha*, *Melica spectabilis*, *Phleum pratense*, *Poa fendleriana*, and *Poa pratense*), *Fragaria virginiana* (Rosaceae), *Senecio integerrimus* and *S. crassulus* (Asteraceae), *Thalictrum fendleri* (Ranunculaceae), *Helianthella quinquenervis* (Asteraceae), *Geranium richardsonii* (Geraniaceae), and *Delphinium barbeyi* (Ranunculaceae); (sites 2 and 3): various grasses (as for site 1), *Heracleum lanatum* (Apiaceae), *Aq-*

uilegia caerulea (Ranunculaceae; not in site 3), *Potentilla gracilis* (Rosaceae), *F. virginiana*, *Angelica grayi* (Apiaceae), *S. integerrimus* and *S. crassulus*, *T. fendleri*, *H. quinquevervis*, and *Mertensia ciliata* (Boraginaceae). Although this list provides a general idea of the plant community, these species may not be parasitized at a rate proportional to their abundance, since hemiparasites can preferentially parasitize some species over others in the field (Gibson and Watkinson 1989, Nilsson and Svensson 1997).

Castilleja miniata individuals grow in discrete rosettes. In all experiments, the presence of alkaloids in Indian paintbrush individuals was determined early in the field season using Dragendorff reagent, which changes color in the presence of quinolizidine alkaloids (Harborne 1984, Stermitz et al. 1989). A positive Dragendorff test indicated that Indian paintbrush were parasitizing *L. argenteus*, since this reagent does not detect alkaloids from any other host species at these sites (*personal observation*). Plants were sampled until an even number was obtained of Indian paintbrush individuals testing positive and negative for alkaloid presence. If alkaloids were not detected, Indian paintbrush was considered to be parasitizing nonlupine host species. It is not possible to determine the hosts of Indian paintbrush that are not parasitizing lupines, since digging out roots would be both laborious and destructive. Indian paintbrush parasitizing lupines and other host species were interspersed at each field site; there were no distinct patches of Indian paintbrush with and without detectable alkaloids.

Indian paintbrush experience little leaf herbivory, but have two common seed predators: larvae of the plume moth *Amblyptilia* (*Platyptilia*) *pica* Walsingham (Pterophoridae) (Lange 1950, McCoy and Stermitz 1983, Roby and Stermitz 1984, Stermitz et al. 1986) and larvae of the fly *Phytomyza subtenella* (Agromyzidae; S. Scheffer, L. S. Adler, and C. Gratton, *unpublished data*). *Amblyptilia pica* is a specialist on *Castilleja* species, and *Phytomyza subtenella* is in a clade that feeds largely on parasitic Scrophulariaceae (S. Scheffer, *personal communication*). Broad-tailed and Rufous Hummingbirds (*Selasphorus platycercus* and *S. rufus*) are the predominant pollinators of Indian paintbrush (*personal observation*). Indian paintbrush and lupines did not share any major pollinators or herbivores during the course of this study (*personal observation*).

Because *C. miniata* plants are long-lived subalpine perennials and could not be manipulated to grow successfully with different hosts, I performed observations and manipulations on established Indian paintbrush in these field studies. Although I could not control for histories or microsite differences between individual plants, this study documents comparative differences in herbivory, pollination, and performance in Indian paintbrush parasitizing lupines vs. other host species.

Herbivory

To determine the effect of host on herbivory, I sampled a total of 65 flowering Indian paintbrush individuals from all three sites in 1996 (20, 25, and 17 plants/site, respectively), and 60 individuals from sites 1 and 2 in 1997 (30 plants/site). Individuals parasitizing lupines were identified using Dragendorff reagent. The two major herbivores, plume moth larvae and agromyzid fly larvae, both feed on inflorescences and leave distinctive damage. Fly larvae remain in one fruit and tunnel through seeds until they emerge at pupation (*personal observation*), while plume moth larvae consume flowers, fruit, and seeds, leaving behind distinctive frass. I measured herbivory by assessing each initiated flower on the longest inflorescence. I recorded the number of seeds and type of damage (none, fly, or moth) for each fruit. I evaluated early bud damage using the presence of bud scars and frass. One potential source of bias is that plume moth larvae may obscure prior fly damage by consuming seeds with fly damage; there was a significant negative correlation between the proportion of fruits scored with damage by plume moth and fly larvae ($\rho = -0.34$, $P < 0.001$, $n = 113$). Thus, I may have underestimated the importance of fly damage. Deer browsed several plants at site 2 in 1997, and the number of inflorescences consumed per plant was recorded.

Herbivory by plume moths and flies was measured as the proportion of fruit damaged per inflorescence and the number of seeds consumed per damaged fruit. I estimated the number of seeds consumed in each damaged fruit using the mean number of seeds produced per undamaged fruit for each plant. Herbivory was analyzed in a three-way ANOVA with host (lupine vs. other hosts) and year as fixed main effects, and site as a random factor (Littell et al. 1991). However, only a subset of plants (50 of 122) had plume moth damage, and these were unbalanced across sites and years. Therefore, only main effects were analyzed for this variable. Because deer browsed only one site in one year, the effect of host on deer browsing was analyzed with a separate one-way ANOVA. I also calculated the correlation of plume moth and fly damage with percentage alkaloid content of Indian paintbrush inflorescences. In all analyses, data were transformed when necessary to meet the assumptions of normality using an arcsine square-root transformation for proportional measures and a logarithmic transformation for numerical data. All ANOVA and MANOVA tests were performed using the GLM procedure of SAS (Littell et al. 1991), and correlations were calculated with the CORR procedure.

To determine the relationship between herbivore performance and alkaloid content of Indian paintbrush, I chose 97 plants at site 1 in 1998. On 24 July, I collected plume moth larvae from Indian paintbrush in a nearby meadow without lupines, randomly assigned one larvae

to one undamaged inflorescence per plant, and placed larvae within fine mesh organdy bags (13×18 cm). On 30 July, 12 and 15 Aug, I recorded the status of each larva (i.e., dead, missing, alive, pupated), and collected and measured the masses of all pupae to the nearest 0.1 mg. On 15 August I also collected between two and five inflorescences per plant for alkaloid analysis. Inflorescences were not collected during the experiment due to the large tissue samples needed for alkaloid analysis and the possibility of inducing changes that could affect herbivory (Karban and Baldwin 1997). I stored pupae in 30-mL (one-ounce) plastic portion cups (Sweetheart Cups, Chicago, Illinois, USA) at room temperature until emergence. Of the 97 initial larvae, 73 pupated and 52 emerged as adults.

I quantified alkaloids using gas chromatography. Tissue was air-dried for several weeks and then ground with a Krups type 203 coffee mill (Krups, Peoria, Illinois, USA). Alkaloids were extracted following the methods of Johnson et al. (1989). The methylene chloride extract was injected into a HP 5890A gas chromatograph (Hewlett Packard, Wilmington, Delaware, USA) with a DB-1 megapore capillary column (30 m, 0.25 mm inner diameter, 0.25 μ m film thickness; J&W Scientific, Folsom, California, USA). Alkaloids were eluted by temperature programming progressing through 200–300°C over a 10-min period, followed by five minutes at 300°C. Alkaloids were identified by comparison to known standards (Johnson et al. 1989).

I used linear regression to determine the relationship between alkaloid concentration and plume moth pupal mass (wet). The relationship between larval status (dead or pupated), pupal eclosion, and alkaloid concentration at the end of the experiment was analyzed with one-way ANOVA.

Pollination

To determine the effect of host species on pollinator visitation, I observed pollinator visits to Indian paintbrush for two seasons. I selected 39 and 62 flowering Indian paintbrush at site 3 in 1997 and 1998, respectively. Using Dragendorff reagent, I identified Indian paintbrush parasitizing lupines, and I bagged plants with loose mesh to prevent removal of nectar when unobserved and to deter herbivory. Herbivores were also regularly removed by hand to minimize effects of herbivory on pollinator preference. I observed all plants at this site simultaneously during the morning when pollinators were most active. I recorded all hummingbird visits, the number of flowers probed, and the time per visit. I observed flowering plants for a total of 30 h in 1997 and 20 h in 1998. In addition, I measured plant height and number of inflorescences twice during each field season and averaged by plant within year for use as covariates.

Pollinator preference was measured as the number of visits to each plant, and the number of flowers probed per visit and time per flower on the subset of visited

plants. The latter two variables were analyzed using MANCOVA, and number of visits was analyzed separately using ANCOVA because of the larger sample size. Independent variables were host (lupine vs. other hosts), year, and the host \times year interaction (all fixed effects), with number of inflorescences and plant height as covariates.

Plant growth and seed production

The same plants used for the herbivory study were also used to measure plant biomass and female fitness. When fruits matured, I collected plants (including major tap root but not fine roots) and measured the number of seeds per undamaged fruit and fruit production for the longest inflorescence. There were 1–16 inflorescences/plant (mean 4.6), 3–29 fruits/inflorescence (mean 13.6), and 5–151 seeds/undamaged fruit (mean 65.3). Due to the time constraints for counting this many seeds (an estimated 857 ± 106 seeds/plant), I used one inflorescence to estimate seed production per plant. Total seed production was estimated by multiplying the number of seeds produced per centimeter of inflorescence by the total length of inflorescences. I used the longest inflorescence, rather than a randomly chosen inflorescence, to provide the most data per inflorescence, and to increase the chance of finding undamaged fruits to estimate seed production. While using the longest inflorescence may have introduced a bias into the results (e.g., if longer inflorescences have lower herbivory or larger seeds), the practice was consistent across samples. In 1996, I measured the mass of a group of 20 seeds from one undamaged fruit per plant to estimate mean seed mass.

Plants are often limited by nitrogen acquisition (Chapin 1980), and one of the benefits for Indian paintbrush of parasitizing a lupine host may be the uptake of fixed nitrogen. I measured nitrogen concentration in vegetative tissues of 30 plants sampled across sites in 1996. Nitrogen analysis is destructive due to the large amount of tissue required; therefore I collected samples at the end of the field season. Samples were dried at 50°C for one week and ground to pass through a 40-mesh screen using a Wiley Mill (Thomas Scientific, Swedesboro, New Jersey). Percent dry mass of nitrogen was measured with a Carlo-Erba combustion gas analyzer (Pella 1990a, b) at the University of California Division of Agriculture and Natural Resources lab. I also measured alkaloid concentration (see *Methods: Herbivory*), and subtracted the proportion of nitrogen in the predominant alkaloids (Adler and Wink 2001) from total nitrogen concentration to determine how much nitrogen could be ascribed to sources other than alkaloids. I calculated the correlation between nonalkaloid nitrogen concentration and Indian paintbrush biomass and seed production.

Biomass and seed number were analyzed using MANOVA with the same model used for the herbivory study. This model was also analyzed with plume moth

TABLE 1. Effect of host species (lupine vs. other species), site, and year on herbivory by plume moth and agromyzid fly larvae in *Castilleja miniata*.

Effect	df	Plume moth				Agromyzid fly			
		Fruits damaged		Seeds consumed		Fruits damaged		Seeds consumed	
		ss	F	ss	F	ss	F	ss	F
Host [‡]	1	0.48	15.93 [†]	2.64	7.34 ^{**}	0.002	0.08	1.56	1454.4 ^{***}
Year [§]	1	0.02	0.05	0.06	0.16	0.31	0.89	1.61	6.82
Site	2	0.26	1.04	1.34	1.86	0.16	0.99	0.44	0.39
Host × Site	2	0.06	0.24	0.06	0.41	0.002	0.00
Host × Year	1	0.03	0.70	0.38	1.98	3.16	2.76
Year × Site	1	0.30	2.40	0.35	4.44 [*]	0.24	0.42
Host × Year × Site	1	0.04	0.33	0.19	2.44	1.15	2.05
Error		14.28	9.62	...	46.34	...
		(103)				(103)		(92)	

Notes: Site was considered a random effect, and year and host species were fixed effects. Measures of herbivory were the proportion of fruits damaged per inflorescence and the number of seeds consumed per damaged fruit. The sample size for seeds consumed per fruit by plume moths was too small to calculate interaction terms, so only main effects were tested. Proportional data were arcsine square-root transformed, and numbers of seeds were log-transformed for analysis. Error df are in parentheses below error ss.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

[†] $P = 0.0574$.

[‡] Tested over the host × site interaction term (except seeds consumed by plume moths).

[§] Tested over the year × site interaction term (except seeds consumed by plume moths).

^{||} Tested over the host × year × site interaction term (except seeds consumed by plume moths).

and agromyzid fly damage (proportion of fruits damaged) included as covariates to determine if the effect of host species on biomass or seeds was due to herbivory. I performed univariate tests when MANOVA analysis revealed significant results of host as a main effect or interaction term (e.g., host × site). Seed mass and whole-plant nitrogen were only measured in one year and were analyzed with two-way ANOVA.

RESULTS

Herbivory

Indian paintbrush that were parasitizing lupines experienced decreased herbivory compared to Indian paintbrush parasitizing other host species. Both plume moth and fly larvae ate significantly fewer seeds per damaged fruit (Table 1, Fig. 1), and plume moth larvae damaged marginally fewer fruits per inflorescence ($P = 0.0574$; Table 1, Fig. 1a). Deer also browsed three times as many inflorescences of Indian paintbrush parasitizing nonlupine host species, compared to Indian paintbrush parasitizing lupines (mean inflorescences browsed ± 1 SE: lupine hosts, 0.71 ± 0.30 ; other hosts 2.19 ± 0.56 ; $F_{1,15} = 9.87$, $P = 0.0078$).

Percent alkaloid content was negatively correlated with the number of seeds consumed per fruit by plume moths ($\rho = -0.33$, $P = 0.026$, $n = 47$), but only marginally negatively correlated with the number of seeds consumed per fruit by fly larvae ($\rho = -0.2$, $P = 0.06$, $n = 87$). There was no significant correlation between alkaloid content and the proportion of fruits damaged by either herbivore ($P > 0.25$ for both herbivores, $n = 105$).

In the separate experiment examining plume moth performance, alkaloid concentration did not correlate with plume moth pupal mass (linear regression; pupal mass: $\beta = 10.23$, $P = 0.1559$, $n = 72$), and there was no effect of alkaloid concentration on eclosion from pupae to adults ($F_{1,80} < 0.001$, $P > 0.95$).

Pollination

Host species did not significantly affect the number of pollinator visits to Indian paintbrush in the field (Table 2; MANCOVA: Wilks' $\lambda = 0.97$, $F_{2,64} = 0.894$, $P = 0.4141$). The number of observed visits to plants was greater for plants with more inflorescences (Table 2) and also varied between years (Fig. 2; MANCOVA host × year interaction: Wilks' $\lambda = 0.89$, $F_{2,64} = 4.00$, $P = 0.0232$). However, when the data were analyzed separately for each year, there were no significant effects of host species on any measure of pollinator preference ($F < 3.0$, $P > 0.1$).

Plant growth and seed production

Combining biomass and seed production in a MANOVA revealed a significant effect of host species that varied across sites, and a significant site effect (site, Wilks' $\lambda = 0.78$, $F_{6,198} = 4.41$, $P < 0.001$; host × site, Wilks' $\lambda = 0.85$, $F_{6,198} = 2.70$, $P = 0.015$). However, there was no significant main effect of host species on biomass and seed production in the MANOVA (Wilks' $\lambda = 0.04$, $F_{2,1} = 12.78$, $P = 0.2$), although Indian paintbrush plants were on average 47% larger and produced over twice as many seeds when parasitizing lupines than when parasitizing other host species. Be-

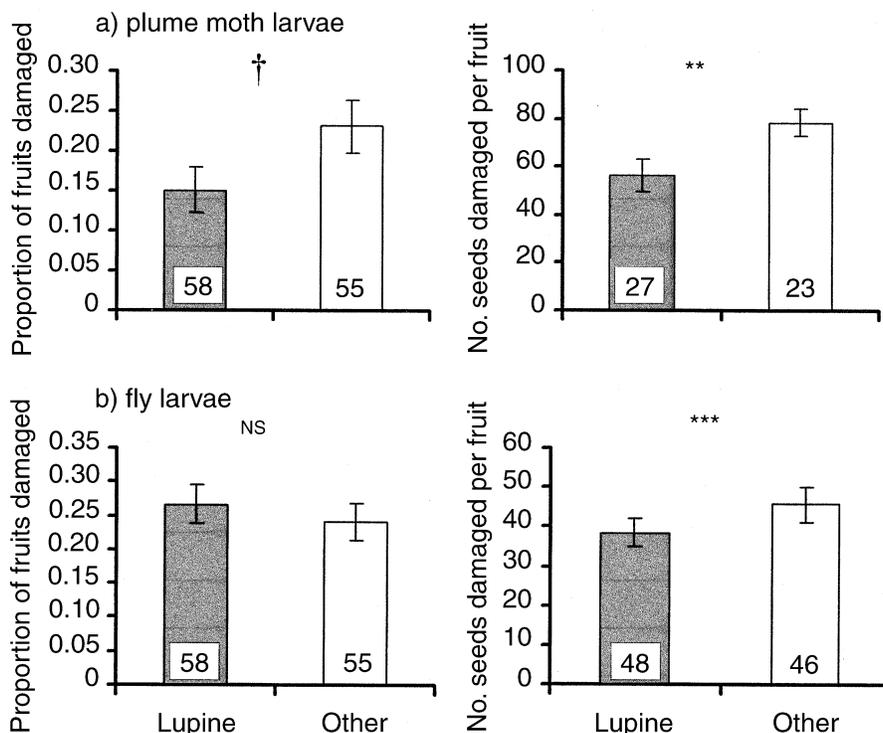


FIG. 1. Effect of host plant on herbivory in the hemiparasite *Castilleja miniata* by (a) plume moth larvae and (b) agromyzid fly larvae. Herbivory was measured as the proportion of fruits damaged per inflorescence and the number of seeds consumed per damaged fruit. Data for each graph are averaged over all other main effects. Error bars represent ± 1 SE, and numbers in columns represent sample size.

† $P < 0.06$; ** $P < 0.01$; *** $P < 0.001$; NS = nonsignificant.

cause the host \times site interaction was significant in the MANOVA, univariate analyses were examined; these showed significant site and host \times site effects on biomass (Table 3, Fig. 3), and a significant main effect of host species on seed production (Table 3, Fig. 4a). Including plume moth and fly herbivory as covariates in the model did not substantially change results for biomass, but did influence the analysis of seed production. Both plume moth damage and fly damage significantly affected seed production ($F_{1,99} = 10.88, P = 0.001$, and

$F_{1,99} = 6.77, P = 0.01$, respectively). When these covariates were included, the effect of host species on seed production was only marginally significant ($F_{1,1} = 11.25, P = 0.08$), suggesting that the increased seed production of Indian paintbrush parasitizing lupine hosts is due partially to a reduction in herbivory.

There was no effect of host species or site on individual seed mass ($F_{1,53} = 0.22, P > 0.68$; Fig. 4b), suggesting that increased seed production is not at the expense of seed quality. Indian paintbrush parasitizing

TABLE 2. Effect of host species (lupine vs. other species), year, number of inflorescences, and plant height on pollinator preference in the field.

Effect	Visits			No. flowers probed per visit			Time per flower probe		
	df	ss	F	df	ss	F	df	ss	F
Host	1	0.48	0.19	1	12.19	1.04	1	0.14	0.51
Year	1	34.57	13.26***	1	413.07	35.25****	1	2.08	7.74**
Host \times Year	1	0.11	0.04	1	65.05	5.55*	1	0.40	1.48
Number of infl.	1	31.38	12.02***	1	5.88	0.50	1	0.052	0.19
Height	1	2.05	0.79	1	22.33	1.91	1	0.065	0.24
Error	91	237.3	...	65	...	761.71	65	17.49	...

Notes: "Visits" represents the number of times that pollinators approached and probed plants. Flowers probed per visit and time per flower probe were analyzed only for plants that were visited by pollinators; i.e., zero values were not included. Number of visits was $\log(x + 1)$ -transformed prior to analysis.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

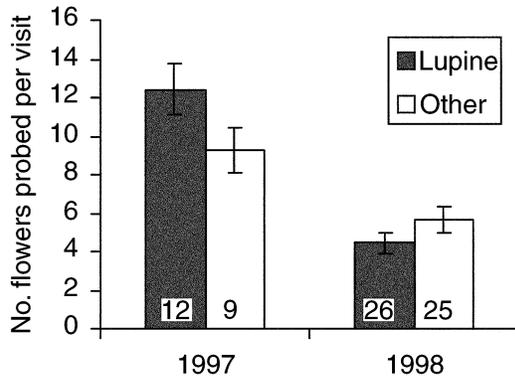


FIG. 2. Effect of host plant and year on pollinator preference in *Castilleja miniata*, measured as the number of flowers probed per visit. Error bars represent ± 1 SE, and numbers in bars represent sample size.

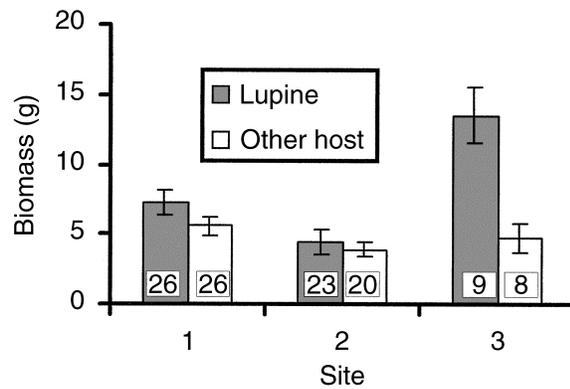


FIG. 3. Effect of host plant and site on biomass of *Castilleja miniata*. Data are averaged over year, except that data at site 3 were collected in 1996 only. Error bars represent ± 1 SE, and numbers in bars represent sample size.

lupines also had marginally higher nitrogen concentration, compared with Indian paintbrush parasitizing other host species ($F_{1,24} = 15.57$, $P = 0.059$; Fig. 4c). Considering only nonalkaloid nitrogen concentration did not change the results; on average alkaloids accounted for only 0.03% of the percent dry mass of nitrogen. There were strong positive correlations between nonalkaloid nitrogen and Indian paintbrush biomass ($\rho = 0.6$, $P < 0.001$, $n = 30$) and seed production ($\rho = 0.43$, $P = 0.017$, $n = 30$).

DISCUSSION

Herbivory

Herbivory by two specialist insect herbivores and one generalist mammalian herbivore was reduced on Indian paintbrush parasitizing lupine hosts, compared to Indian paintbrush parasitizing other host species. There was a negative correlation between herbivory by both insects and alkaloid concentration of inflorescences, suggesting that the mechanism of reduced herbivory is alkaloid uptake from lupine hosts. While

proximity of Indian paintbrush to alkaloid-containing lupines is another possible mechanism, this seems unlikely since both insect herbivores are specialists that spend their larval development on one host plant (Stermitz et al. 1986, *personal observation*). This result is consistent with experiments in another *Castilleja-Lupinus* system, in which experimentally manipulated alkaloid uptake reduced floral herbivory by the herbivore *Endotheria hebesana* (Lepidoptera: Tortricidae) (Adler 2000a). Thus, the benefits for Indian paintbrush of parasitizing lupine include reduced herbivory and may therefore vary between populations that vary in herbivore pressure.

Lupine alkaloids are generally detrimental and act to deter a wide range of organisms, including vertebrate and invertebrate herbivores and microbes (reviewed in Wink 1992, 1993). Although Indian paintbrush parasitizing lupines had reduced plume moth herbivory, no clear relationship emerged between alkaloid content of inflorescences and herbivore performance. Several hypotheses can be proposed to explain this lack of effect:

TABLE 3. Effect of host species (lupine vs. other species), sites, and year on biomass and estimated seed production in *Castilleja miniata*.

Effect	Biomass			Seeds		
	df	ss	F	df	ss	F
Host†	1	3.77	1.51	1	4.35	39.19*
Year‡	1	7.78	38.94	1	67.63	4.27
Site	2	7.80	7.75***	2	15.74	2.38
Host × Site	2	4.99	4.96**	2	0.22	0.03
Host × Year§	1	0.53	3.55	1	0.43	0.49
Year × Site	1	0.20	0.40	1	15.84	4.78*
Host × Year × Site	1	0.15	0.30	1	0.89	0.27
Error	101	50.82	...	101	334.67	...

Notes: Site was considered a random effect, and year and host plant were fixed effects. Data were log transformed prior to analysis.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† Tested over the host × site interaction term.

‡ Tested over the year × site interaction term.

§ Tested over the host × year × site interaction term.

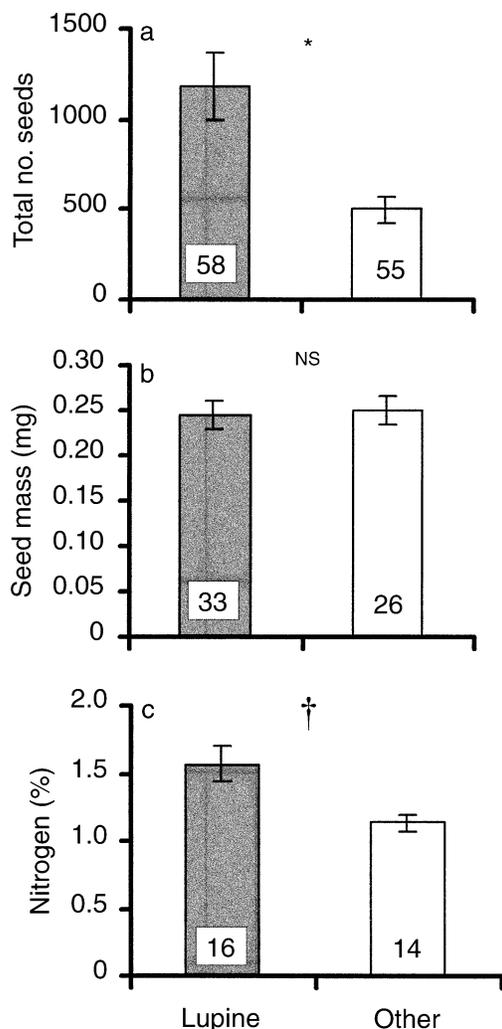


FIG. 4. Effect of host plant on (a) estimated total seed production, (b) mean seed mass, and (c) percentage total nitrogen by dry mass in *Castilleja miniata*. Data for (a) are from 1996 and 1997 combined, and data for (b) and (c) are from 1996 only. Data for each graph are averaged over all other main effects. Error bars represent ± 1 SE, and numbers in bars represent sample size.

† $P < 0.06$; * $P < 0.05$; NS = nonsignificant.

(1) alkaloid content may be detrimental to larval performance, but correlated with other positive effects of lupine hosts, such as increased nitrogen, that obscure this effect; (2) alkaloid uptake may reduce adult oviposition preference, but have no effect on herbivore performance (Thompson and Pellmyr 1991); (3) the reduced herbivory of Indian paintbrush parasitizing lupines may be due to some effect other than alkaloid uptake; for example, increased nitrogen concentration may translate to less food required for herbivore development; and/or (4) variation in larval response to alkaloids or in the ability to accurately quantify alkaloids may obscure any effect of alkaloids on larval performance. Although studies of the congeneric hemi-

parasite *Castilleja indivisa* indicate that alkaloids play an important role in resistance to herbivory (Adler 2000a), it is not possible to distinguish among these hypotheses without being able to manipulate alkaloids in *C. miniata*.

The effect of host species with alkaloids, compared to hosts without alkaloids, on herbivory in parasitic plants has not been consistent in other studies. Both generalist and specialist herbivores (larvae of *Trichoplusia ni* and *Euphydryas anicia*, respectively) performed more poorly in the laboratory on a diet of *Castilleja sulphurea* containing alkaloids from the host *Delphinium occidentale*, compared with leaves from nonalkaloid *C. sulphurea* (Marko et al. 1995). Conversely, in a greenhouse study, aphids survived and reproduced best on *Castilleja wightii* parasitizing the alkaloid-containing host *Lupinus arboreus*, compared to *C. wightii* parasitizing two nonleguminous, nonalkaloid host species (Marvier 1996). Increased total nitrogen in parasites on lupines may have been more important to aphids than the presence of alkaloids (Kyto et al. 1996). In a field study, alkaloid uptake in the hemiparasite *Pedicularis semibarbata* from the host *Lupinus fulcratus* did not affect oviposition or larval performance by the specialist herbivore *Euphydryas editha*, compared to *Pedicularis* parasitizing other host species (Stermitz et al. 1989). These studies indicate that herbivore preference and performance on hemiparasites is not always predicted by the alkaloid content of host species.

Pollination

Pollinators did not discriminate between *C. miniata* parasitizing different host species in the field. Thus, while lupines reduce herbivory on Indian paintbrush, there was no evidence for indirect effects of hosts on parasites via pollinator preference. In a separate experiment, hand pollination of Indian paintbrush flowers did not increase *C. miniata* seed set at one site in 1998 (L. Adler, unpublished data), suggesting that seed production is limited by resources rather than by pollen transfer, at least in some years or sites. Therefore, pollinator preference may not affect hemiparasite female fitness, even if pollinators did discriminate between Indian paintbrush with different hosts.

Alkaloid-containing hosts have the potential to either increase or decrease pollinator attraction to hemiparasites via different mechanisms. In some plant species, resistance to herbivores may cause decreased pollinator attraction due to secondary compounds in floral structures (Strauss et al. 1999, Adler 2000b). Neither *Castilleja miniata* nor *Castilleja indivisa* contained alkaloids in nectar when parasitizing alkaloid-containing hosts (Adler and Wink 2001). It is therefore not surprising that lupine hosts did not deter pollinators of either *Castilleja* species. However, norditerpenoid alkaloids from the host *Delphinium occidentale* have been found in the nectar of the hemiparasite *Castilleja*

sulphurea (Marko and Stermitz 1997). It would be interesting to determine whether host association influences pollinator preference in this closely related hemiparasite.

Alkaloid uptake from host plants could also increase pollinator attraction to hemiparasites by reducing herbivory. Reduced floral herbivory resulted in twice as many pollinator visits to *Castilleja indivisa* parasitizing high-alkaloid compared to low-alkaloid lines of a lupine host (Adler et al. 2001). However, in the current study of *C. miniata*, herbivores were removed from Indian paintbrush in the pollination experiment to avoid confounding herbivore effects with pollinator effects. Thus, while alkaloids in *C. miniata* were not directly attractive to pollinators, there is still the possibility that alkaloid uptake could increase pollinator attraction indirectly via reduced plume moth herbivory in inflorescences.

Plant growth and seed production

Indian paintbrush benefited from parasitizing lupine hosts, compared to other host species. Indian paintbrush parasitizing lupines produced more seeds across two years of sampling and had greater biomass, although the extent of this effect varied between sites. These benefits are most likely to arise from reduced seed predation, which strongly affected seed production and was consistently reduced by parasitizing lupines, and possibly by the marginal increase in nitrogen concentration. However, the variation in biomass across sites suggests that the interaction of these effects may be complex. While it is not possible without extensive manipulations to determine why such differences in plant biomass existed across nearby sites, variation in abiotic resources is a possible explanation. Indian paintbrush at site 2, a dry and shady site, had the lowest overall biomass; while Indian paintbrush at site 1, which was dry but sunnier, had moderate biomass. The largest plants and the strongest host effects were at site 3, which in addition to being sunny was also moist and slightly lower in elevation. Thus, the benefits of parasitizing lupines appear to be strongest at the site with the most available resources for growth.

Population- and community-level consequences

In this study, *C. miniata* had reduced herbivory and increased seed set when parasitizing lupine hosts compared to all other host species combined. Since many parasitic plants have greater fitness on a subset of potential hosts, the question arises of whether generalist parasites, like generalist herbivores, can evolve races that specialize on beneficial hosts. While some studies have documented host preference in generalist parasitic plants (Werth and Riopel 1979, Gibson and Watkinson 1989, Kelly 1990, 1992, Nilsson and Svensson 1997, Yoder 1997, Norton and De Lange 1999), for host preference to evolve in response to selection there must be heritable variation in this trait (Falconer 1989). Intra-

specific variation in parasitic plant host preference has only been examined in one study to my knowledge. Maternal sibships of the annual hemiparasite *Triphysaria pusilla* varied in their preference for a lupine host (*L. nanus*) compared to a grass host (*Bromus carinatus*) (Adler 2000c). However, this variation appears to be determined more by maternal host than by genetic variation, suggesting that specialization is unlikely to evolve. In an unpredictable environment dominated by annuals, maintaining a plastic response to hosts may be the most appropriate strategy; no studies have examined whether perennial parasites have similar strategies.

Parasitic plants are found in every major ecosystem (Kuijt 1969), and their presence can alter community composition and structure (Bennets et al. 1996, Pennings and Callaway 1996, Marvier 1998b). Several studies, including the present one, have found that hemiparasites are most successful on leguminous hosts (Gibson and Watkinson 1989, Seel and Press 1993, 1994, Matthies 1996, Press and Seel 1996, Marvier 1998a). Hemiparasites can also alter the competitive outcome between host species by having the most detrimental impact on the species that is both the most beneficial host and strongest competitor, typically a legume (Gibson and Watkinson 1991, Matthies 1996). By reducing the competitive superiority of legumes that can alter community dynamics and increase the invasion of non-native species via nitrogen fixation (Maron and Jefferies 1999), parasitic plants may play an important role in maintaining species diversity at the community level. The present study demonstrates that host-parasite plant interactions have important consequences not just for host plants, but also for parasitic plants and animals, such as herbivores interacting with those parasites. Thus, parasitic plant-host plant interactions may alter community composition via several mechanisms.

ACKNOWLEDGMENTS

I thank Judah Dinnel, Susie Geer, and Amy Kreutzer for their hard work in the field, Barbara L. Bentley and Michael Ziebell for invaluable assistance with alkaloid analysis, including the use of B. L. Bentley's gas chromatograph (funded by USDA/National Resources Inventory [NRI] Grant 9401661), Nick Waser, Mary Price, and Bill Calder for hummingbird advice, and Kevin Taylor, David Inouye, Mary Price and Rick Williams for host plant identifications. The Rocky Mountain Biological Laboratory provided facilities. Anurag Agrawal, Keith Clay, Becky Irwin, Rick Karban, Kevin Rice, Jennifer Rudgers, Maureen Stanton, Sharon Strauss, Jennifer Thaler, Nora Underwood, Paige Warren, and four anonymous reviewers provided helpful comments on the manuscript. This research was funded by a Center for Population Biology Research Award, Jastro-Shields Research Award, Sigma Xi Grants-in-Aid of Research, National Science Foundation Graduate Research Fellowship, and National Science Foundation Dissertation Improvement Grant DEB 98-00885.

LITERATURE CITED

Adler, L. S. 2000a. Alkaloid uptake increases fitness in a hemiparasitic plant via reduced herbivory and increased pollination. *American Naturalist* **156**:92–99.

- Adler, L. S. 2000b. The ecological significance of toxic nectar. *Oikos* **91**:409–420.
- Adler, L. S. 2000c. Herbivory and pollination in hemiparasitic plants: effects of host plant and host-obtained alkaloids. Dissertation. University of California–Davis, California, USA.
- Adler, L. S., R. Karban, and S. Y. Strauss. 2001. Direct and indirect effects of alkaloids on plant fitness via herbivory and pollination. *Ecology* **82**:2032–2044.
- Adler, L. S., and M. Wink. 2001. Transfer of alkaloids from hosts to hemiparasites in two *Castilleja*–*Lupinus* associations: analysis of floral and vegetative tissues. *Biochemical Systematics and Ecology* **29**:551–561.
- Arslanian, R. L., G. H. Harris, and F. R. Stermitz. 1990. New quinolizidine alkaloids from *Lupinus argenteus* and its hosted root parasite *Castilleja sulphurea*: stereochemistry and conformation of some naturally occurring cyclic carbinolamides. *Journal of Organic Chemistry* **55**:1204–1210.
- Baemel, P., L. Witte, P. Proksch, and F. C. Czygan. 1992. Uptake and metabolism of host plant alkaloids by parasitizing *Cuscuta* species. *Planta Medica* **58**:A671.
- Bennetts, R. E., G. C. White, F. G. Hawksworth, and S. E. Severs. 1996. The influence of dwarf mistletoe on bird communities in Colorado ponderosa pine forests. *Ecological Applications* **6**:899–909.
- Boros, C. A., D. R. Marshall, C. R. Caterino, and F. R. Stermitz. 1991. Iridoid and phenylpropanoid glycosides from *Orthocarpus* spp.: Alkaloid content as a consequence of parasitism on *Lupinus*. *Journal of Natural Products (Lloydia)* **54**:506–513.
- Chapin, F. S. I. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**:233–260.
- Chew, F. S., and J. E. Rodman. 1979. Plant resources for chemical defense. Pages 271–308 in G. A. Rosenthal and D. H. Janzen, editors. *Herbivores: their interactions with secondary plant metabolites*. Academic Press, New York, New York, USA.
- Davies, D. M., and J. D. Graves. 1998. Interactions between arbuscular mycorrhizal fungi and the hemiparasitic angiosperm *Rhinanthus minor* during co-infection of a host. *New Phytologist* **139**:555–563.
- Falconer, D. S. 1989. *Introduction to quantitative genetics*. Third edition. Longman Scientific and Technical, New York, New York, USA.
- Fowden, L., and P. J. Lea. 1979. Mechanism of plant avoidance of autotoxicity by secondary metabolites, especially by nonprotein amino acids. Pages 135–160 in G. A. Rosenthal and D. H. Janzen, editors. *Herbivores: their interactions with secondary plant metabolites*. Academic Press, New York, New York, USA.
- Gibson, C. C., and A. R. Watkinson. 1989. The host range and selectivity of a parasitic plant: *Rhinanthus minor* L. *Oecologia* **78**:401–406.
- Gibson, C. C., and A. R. Watkinson. 1991. Host selectivity and the mediation of competition by the root hemiparasite *Rhinanthus minor*. *Oecologia* **86**:81–87.
- Graves, J. D. 1995. Host-plant responses to parasitism. Pages 292 in M. C. Press and J. D. Graves, editors. *Parasitic plants*. Chapman and Hall, London, UK.
- Harborne, J. B. 1984. *Phytochemical methods: a guide to modern techniques of plant analysis*. Second edition. Chapman and Hall, London, UK.
- Jeschke, W. D., P. Baemel, N. Rath, F. C. Czygan, and P. Proksch. 1994. Modelling of the flows and partitioning of carbon and nitrogen in the holoparasite *Cuscuta reflexa* Roxb. and its host *Lupinus albus* L. II. Flows between host and parasite and within the parasitized host. *Journal of Experimental Botany* **45**:801–812.
- Johnson, N. D., L. P. Rigney, and B. L. Bentley. 1989. Short-term induction of alkaloid production in lupines: differences between nitrogen-fixing and nitrogen-limited plants. *Journal of Chemical Ecology* **15**:2425–2434.
- Karban, R., and I. T. Baldwin. 1997. *Induced responses to herbivory*. University of Chicago Press, Chicago, Illinois, USA.
- Kelly, C. K. 1990. Plant foraging: a marginal value model and coiling response in *Cuscuta subinclusa*. *Ecology* **71**:1916–1925.
- Kelly, C. K. 1992. Resource choice in *Cuscuta europaea*. *Proceedings of the National Academy of Sciences* **89**:12194–12197.
- Kuijt, J. 1969. *The biology of parasitic flowering plants*. University of California Press, Berkeley, California, USA.
- Kyto, M., P. Niemela, and S. Larsson. 1996. Insects on trees: population and individual response to fertilization. *Oikos* **75**:148–159.
- Lange, W. H. 1950. Biology and systematics of plume moths of the genus *Platyptilia* in California. *Hilgardia* **19**:561–668.
- Littell, R. C., R. J. Freund, and P. C. Spector. 1991. *SAS system for linear models*. Third edition. SAS Institute, Cary, North Carolina, USA.
- Marko, M. D., M. F. Antolin, and F. R. Stermitz. 1995. The effect of incorporated delphinium alkaloids by *C. sulphurea* on a generalist and a specialist insect herbivore. *Bulletin of the Ecological Society of America* **76**:168.
- Marko, M. D., and F. R. Stermitz. 1997. Transfer of alkaloids from *Delphinium* to *Castilleja* via root parasitism. *Norditerpenoid alkaloid analysis by electrospray mass spectrometry*. *Biochemical Systematics and Ecology* **25**:279–285.
- Maron, J. L., and R. L. Jefferies. 1999. Bush lupine mortality, altered resource availability, an alternative vegetation states. *Ecology* **80**:443–454.
- Marvier, M. A. 1995. Host use by parasitic plants: effects on insect herbivore performance in a coastal plant community. *Bulletin of the Ecological Society of America* **76**:361–362.
- Marvier, M. A. 1996. Parasitic plant–host interactions: plant performance and indirect effects on parasite-feeding herbivores. *Ecology* **77**:1398–1409.
- Marvier, M. 1998a. A mixed diet improves performance and herbivore resistance of a parasitic plant. *Ecology* **79**:1272–1280.
- Marvier, M. A. 1998b. Parasite impacts on host communities: plant parasitism in a California coastal prairie. *Ecology* **79**:2616–2623.
- Matthies, D. 1995. Host–parasite relations in the root hemiparasite *Melampyrum arvense*. *Flora* **190**:383–394.
- Matthies, D. 1996. Interactions between the root hemiparasite *Melampyrum arvense* and mixtures of host plants: heterotrophic benefit and parasite-mediated competition. *Oikos* **75**:118–124.
- McCoy, J. W., and F. R. Stermitz. 1983. Alkaloids from *Castilleja miniata* and *Penstemon whippleanus*, two host species for the plume moth, *Amblyptilia (Platyptilia) pica*. *Journal of Natural Products* **46**:902–907.
- McKey, D. 1974. Adaptive patterns in alkaloid physiology. *American Naturalist* **108**:305–320.
- Mead, E. W., M. Looker, D. R. Gardner, and F. R. Stermitz. 1992. Pyrrolizidine alkaloids of *Liatris punctata* and its root parasite, *Castilleja integra*. *Phytochemistry* **31**:3255–3257.
- Miller, T. E., and J. Travis. 1996. The evolutionary role of indirect effects in communities. *Ecology* **77**:1329–1335.
- Nilsson, C. H., and B. M. Svensson. 1997. Host affiliation in two subarctic hemiparasitic plants: *Bartsia alpina* and *Pedicularis lapponica*. *Ecoscience* **4**:80–85.
- Norton, D. A., and P. J. De Lange. 1999. Host specificity in parasitic mistletoes (Loranthaceae) in New Zealand. *Functional Ecology* **13**:552–559.

- Pella, E. 1990a. Elemental organic analysis. Part 1: historical developments. *American Laboratory* **22**:116.
- Pella, E. 1990b. Elemental organic analysis. Part 2: state of the art. *American Laboratory* **22**:28.
- Pennings, S. C., and R. M. Callaway. 1996. Impact of a parasitic plant on the structure and dynamics of salt marsh vegetation. *Ecology* **77**:1410–1419.
- Press, M. C., and J. D. Graves. 1995. *Parasitic plants*. Chapman and Hall, London, UK.
- Press, M. C., and W. E. Seel. 1996. Interactions between hemiparasitic angiosperms and their hosts in the subarctic. Pages 151–158 in P. S. Karlsson and T. V. Callaghan, editors. *Ecological Bulletins*, no. 45. Plant ecology in the subarctic Swedish Lapland. Munksgaard, Copenhagen, Denmark.
- Roby, M. R., and F. R. Stermitz. 1984. Pyrrolizidine and pyridine monoterpene alkaloids from two *Castilleja* plant hosts of the plume moth, *Platyptilia pica*. *Journal of Natural Products* **47**:846–853.
- Schneider, M. J., and F. R. Stermitz. 1990. Uptake of host plant alkaloids by root parasitic *Pedicularis* spp. *Phytochemistry* **29**:1811–1814.
- Schoener, T. W. 1993. On the relative importance of direct versus indirect effects in ecological communities. Pages 365–411 in H. Kawanabe, J. E. Cohen, and K. Iwasaki, editors. *Mutualism and community organization: behavioural, theoretical, and food-web approaches*. Oxford University Press, Oxford, UK.
- Seel, W. E., and M. C. Press. 1993. Influence of the host on three sub-Arctic annual facultative root hemiparasites: I. Growth, mineral accumulation and above-ground dry-matter partitioning. *New Phytologist* **125**:131–138.
- Seel, W. E., and M. C. Press. 1994. Influence of the host on three sub-Arctic annual facultative root hemiparasites: II. Gas exchange characteristics and resource use-efficiency. *New Phytologist* **127**:37–44.
- Seel, W. E., and M. C. Press. 1996. Effect of repeated parasitism by *Rhinanthus minor* on the growth and photosynthesis of a perennial grass, *Poa alpina*. *New Phytologist* **134**:495–502.
- Silva, A., and C. Martinez Del Rio. 1996. Effects of the mistletoe *Tristerix aphyllus* (Loranthaceae) on the reproduction of its cactus host *Echinopsis chilensis*. *Oikos* **75**:437–442.
- Stermitz, F. R., G. N. Belofsky, D. Ng, and M. C. Singer. 1989. Quinolizidine alkaloids obtained by *Pedicularis semibarbata* (Scrophulariaceae) from *Lupinus fulcratus* (Leguminosae) fail to influence the specialist herbivore *Euphydryas editha* (Lepidoptera). *Journal of Chemical Ecology* **15**:2521–2530.
- Stermitz, F. R., T. A. Foderaro, and Y. X. Li. 1993. Iridoid glycoside uptake by *Castilleja integra* via root parasitism on *Penstemon teucrioides*. *Phytochemistry* **32**:1151–1153.
- Stermitz, F. R., and G. H. Harris. 1987. Transfer of pyrrolizidine and quinolizidine alkaloids to *Castilleja* (Scrophulariaceae) hemiparasites from composite and legume host plants. *Journal of Chemical Ecology* **13**:1917–1925.
- Stermitz, F. R., G. H. Harris, and W. Jing. 1986. Iridoids and alkaloids from *Castilleja* host plants for *Platyptilia pica*. Rhexifoline content of *P. pica*. *Biochemical Systematics and Ecology* **14**:499–506.
- Stermitz, F. R., and M. Pomeroy. 1992. Iridoid glycosides from *Castilleja purpurea* and *C. indivisa*, and quinolizidine alkaloid transfer from *Lupinus texensis* to *C. indivisa* via root parasitism. *Biochemical Systematics and Ecology* **20**:473–475.
- Strauss, S. Y. 1991. Indirect effects in community ecology: their definition, study and importance. *Trends in Ecological Evolution* **6**:206–210.
- Strauss, S. Y., D. H. Siemens, M. B. Decher, and T. Mitchell-Olds. 1999. Ecological costs of plant resistance to herbivores in the currency of pollination. *Evolution* **53**:1105–1113.
- Thompson, J. N., and O. Pellmyr. 1991. Evolution of oviposition behavior and host preference in Lepidoptera. *Annual Review of Entomology* **36**:65–90.
- Werth, C. R., and J. L. Riopel. 1979. A study of the host range of *Aureolaria pedicularia* (L.) Raf. (Scrophulariaceae). *American Midland Naturalist* **102**:300–306.
- Wink, M. 1992. The role of quinolizidine alkaloids in plant–insect interactions. Pages 133–169 in E. Bernays, editor. *Insect–plant interactions*. CRC Press, Boca Raton, Florida, USA.
- Wink, M. 1993. Allelochemical properties or the raison d’être of alkaloids. Pages 1–118 in G. A. Cordell, editor. *The alkaloids*. Academic Press, San Diego, California, USA.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* **25**:443–466.
- Yoder, J. I. 1997. A species-specific recognition system directs haustorium development in the parasitic plant *Trichophysaria* (Scrophulariaceae). *Planta* **202**:407–413.