PARASITE IMPACTS ON HOST COMMUNITIES: PLANT PARASITISM IN A CALIFORNIA COASTAL PRAIRIE

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Abstract. Generalized parasites may strongly influence host communities by differentially impacting host species. However, the community effects of an important and widespread group of generalized parasites, the parasitic plants, have been poorly studied. I performed removal experiments to assess the role of a small annual hemiparasite, *Triphysaria pusilla* (Scrophulariaceae), in a California coastal prairie community.

Removal of *Triphysaria* led to increased total biomass of the host assemblage; this effect was largely attributable to a substantial increase in the biomass of graminoids. In addition, host suitability differed dramatically among three annual taxa: *Triphysaria* parasitizing grass hosts produced 3.2 and 6.4 times more fruits, on average, than those attacking two dicot hosts, *Hypochaeris glabra* and *Lupinus nanus,* respectively. Availability of multiple host species failed to improve parasite performance beyond that achieved on grasses alone. *Triphysaria* impacts also differed greatly among host species: natural densities of *Triphysaria* significantly reduced the dry mass of grasses, while *Hypochaeris* and *Lupinus* were unharmed.

In addition to these direct effects, I tested whether *Triphysaria* attack influenced competitive interactions among host taxa. Natural densities of grasses significantly reduced growth and fecundity of *Hypochaeris* and *Lupinus,* suggesting that the presence of *Triphysaria* in mixed stands of hosts might allow competitive release of these dicot species. However, the combination of grasses and *Triphysaria* caused a more severe reduction in *Lupinus* performance than that caused by grasses alone. Thus, observations of direct effects among pairs of species were not sufficient to explain either the outcome or intensity of multi-species interactions. Taken together, these experiments demonstrate that a generalist plant parasite can influence the structure of a natural plant community, and that interactions between a generalist parasite and its multiple host species can be difficult to predict from studies that consider only single host taxa.

Key words: coastal prairie; competition; generalist; parasitic plant; parasitism; Triphysaria pusilla.

INTRODUCTION

The exquisite adaptations of many parasite species to find and exploit particular hosts make parasites among the best examples of highly specialized heterotrophs. However, many parasites are in fact generalists, exploiting from several to dozens of host species. Further, it is these generalist parasites that have most often been implicated as major shapers of community structure (Anderson 1972, van Riper et al. 1986, Schmitz and Nudds 1993; reviewed in Dobson and Hudson 1986, Price et al. 1986, Minchella and Scott 1991, Dobson and Crawley 1994, McCallum and Dobson 1995). Because generalized parasites can be supported by multiple hosts, and because hosts will differ in susceptibility to attack, generalists are likely to alter competitive interactions among hosts (e.g., Park 1948) and create strong indirect effects, such as apparent competition (Price et al. 1988). One of the most ubiquitous groups of generalist parasites, the parasitic plants, has rarely been studied by ecologists, and particularly not with regard to community-wide effects. Here, I present an experimental analysis of the population and community effects of a generalist plant parasite in a California coastal prairie community.

Parasitic plants are likely to play an important role in determining the structure of a wide variety of plant communities because they frequently cause different amounts of harm to particular host species, and because parasite performance can vary greatly depending on which host is used (e.g., Wilkins 1963, Atsatt and Strong 1970, Chuang and Heckard 1971, Snogerup 1982, Gibson and Watkinson 1991, Seel and Press 1993, Seel et al. 1993). Further, some parasitic plants demonstrate preferences for particular host species (Gibson and Watkinson 1989, Kelly 1990). However, while there are over 3000 species of parasitic plants occurring in a wide variety of natural plant communities (Kuijt 1969, Atsatt 1983, Press 1989), community-level effects have been examined for only a few

parasitic plant taxa. These earlier studies demonstrate that parasitic plants can reduce total yield, alter species diversity, and cause cycles in vegetation (ter Borg and Bastiaans 1973, Gibson and Watkinson 1992, Pennings and Callaway 1996). Building on these studies, I have examined interactions of pairs and trios of species in the field to unravel the complex effects of a plant parasite on its host community.

Here I report the results of two years of field manipulations in which I investigated the role of the small, annual hemiparasite, *Triphysaria pusilla* (Benth.) Chuang & Heckard (formerly known as *Orthocarpus pusillus*; Scrophulariaceae; hereafter, *Triphysaria*) in a coastal prairie community. I performed removal experiments to assess the effects of *Triphysaria* (1) on the entire suite of potential host species, (2) on particular host taxa, and (3) on competitive interactions among host species. These experiments address the realistic situation of simultaneous attack by parasite individuals of multiple host species in a manipulated, yet natural setting, while closely examining interactions among key pairs and trios of species. Taken together, these field manipulations address how different host species are affected by parasitism in the field, how *Triphysaria* performance is affected by different host environments, and whether this small generalist parasite can influence the structure of its natural host community.

METHODS

Study site and natural history

This work was conducted at the Bodega Marine Reserve, Sonoma County, California, located on a small coastal peninsula ~100 km north of San Francisco, California. The coastal prairie at this site is ~2.5 km^2, and there are gradients in temperature and soil characteristics that lead to rapid changes in vegetation as one moves inland from the coastal bluffs (Barbour 1973). I performed my experiments several hundred meters from the bluffs in an area protected from direct ocean exposure. This area is dominated by annual species: annuals constituted 70.5 ± 2.3% (mean ± 1 SE) of the dicot biomass (not including *Triphysaria*) harvested in the parasite removal experiment, and annual grasses made up 86.5 ± 2.4% of graminoid biomass (based on a pilot study with 20 plots; M. A. Marvier, *unpublished data*). Approximately three-fourths of the plant species are annual and over half are introduced from Europe (Appendix). Most coastal prairie species germinate during the wet winter months (November–March) and senesce in late spring (May–June) as summer drought approaches.

The parasitic plants at this site, mostly *Triphysaria pusilla* (but also a few *T. eriantha* individuals), are small annuals (generally <10 cm tall), and thus are very similar to the majority of available hosts in both size and life span. *Triphysaria* are hemiparasitic root

parasites that obtain water and nutrients from the roots of neighboring plants. Although *Triphysaria* contain chlorophyll and are capable of photosynthesis, it is unlikely that these plants could thrive without a host in nature (see *Results*). From excavation and examination of haustoria, I have determined that *Triphysaria* are generalist parasites, potentially affecting a broad diversity of angiosperm hosts (*personal observation*).

Parasite removals

To examine the role of *Triphysaria* in the coastal prairie community, I selected 21 blocks, each 1 × 1 m, of low-growing prairie vegetation in early March 1994 after most germination was complete. I divided each block into four 0.25-m^2 plots and removed *Triphysaria* from two of these plots. Treatments were arranged along diagonals to maximize interspersion of treatments. Thus, each 1-m^2 block contained two replicates of each treatment (n = 42 plots per treatment). To minimize disturbance, *Triphysaria* seedlings were carefully plucked out with tweezers. Additional removal of later-germinating *Triphysaria* was performed as needed.

In late May, after most annual species had completed flowering, I harvested the aboveground portion of all plants and recorded the dry mass for each species separately, with the exception of the graminoids, which could not be accurately sorted to species after harvest. Measures reported here are for a 0.0625-m^2 sampling quadrat centered within each plot. This smaller sampling area was used to provide a 12.5-cm border around the sampled area, ensuring that parasites from outside the plots would not influence the results. This relatively small sampling area corresponds well to the small size and short rooting distance of individual plants in this community; sampling quadrats always contained >100 individual plants and an average of >12 plant species.

To test for community-level effects of parasitism, I compared the total yield of all hosts combined, the biomass of each host taxon, and the number of host species in removal vs. control plots. I used a one-way ANOVA with complete blocks to examine each of these variables. Because in this study blocks represent a random effect, I used the mean squares of the block by treatment interaction as the error term for tests of treatment effects (Newman et al. 1997). Data were log transformed as needed to satisfy the assumption of homoscedasticity. Finally, I calculated the Shannon-Wiener index of species diversity for each plot and used a sign test to examine whether *Triphysaria* removal altered host diversity in any consistent direction.

Manipulations of parasites and hosts

To more carefully examine host–parasite interactions, I focused on only three host taxa in 1995. In addition to effects of *Triphysaria* on various host species, I also evaluated (1) the effect of different hosts and host combinations on *Triphysaria* performance and

TABLE 1. The 11 experimental treatments used in the 1995 study (x = present, − = absent).

Parasite (*Triphysaria pusilla*)	Host taxa		
	Grasses	*Hypochaeris glabra*	*Lupinus nanus*
x	−	−	−
x	x	−	−
x	−	x	−
x	−	−	x
x	x	x	−
x	x	−	x
−	x	−	−
−	−	x	−
−	−	−	x
−	x	x	−
−	x	−	x

(2) the competitive interactions among pairs of hosts in the presence and absence of *Triphysaria*.

I concentrated on the three most abundant annual host taxa: a native, nitrogen-fixing annual, *Lupinus nanus*; an introduced annual, *Hypochaeris glabra* (Asteraceae); and a mix of mostly introduced annual grasses. Because it was difficult to identify grasses to species before flowering and because the grasses all have fine, fibrous roots, I combined the grass species into a group that may act as functionally similar hosts for *Triphysaria*. Listed from most to least common, the grasses included: *Aira caryophyllea, Vulpia bromoides, Lolium perenne, Avena barbata, Bromus diandrus,* and *Bromus hordeaceus.*

On 21 January 1995, I searched for 10 areas at least 1.5 m in diameter that contained seedlings of all four focal taxa: *Triphysaria, Lupinus, Hypochaeris,* and grasses. Each of these 10 areas represented an experimental block. Within each block, I established 11 separate experimental plots by pounding 20 cm diameter rings of lawn edging into the soil to a depth of 12 cm. These barriers effectively isolated the root systems within each plot (M. A. Marvier, *personal observation*). In addition, I covered each plot with wire caging to prevent grazing by rabbits and deer.

I randomly assigned each plot within each block to one of the 11 experimental treatments (Table 1). Thus, each treatment was replicated 10 times for a total of 110 plots. The experimental treatments included three types of pure stands of hosts (*Lupinus, Hypochaeris,* or grasses) and two types of mixed stands of hosts (grasses with either *Lupinus* or *Hypochaeris*). I did not include the combination of *Lupinus* and *Hypochaeris,* because results of the 1994 removal study led me to expect that the most important parasite effects would involve grasses. I also included a treatment of *Triphysaria* grown in the absence of any hosts to assess the extent of host dependence for this partially autotrophic parasite.

On 21 and 22 January, I used tweezers to pluck out all nonfocal species from each plot, leaving those species appropriate to the assigned treatment at their ambient densities. I continued to remove nonfocal species from all plots every 2–3 weeks from 4 February through 10 May 1995. Because the experimental plots tended to dry out faster than the surrounding vegetation, I watered all plots on 4 and 18 February and 1 April. To assess whether there were any initial differences among the experimental treatments, I recorded the number of individuals of *Lupinus, Hypochaeris,* and *Triphysaria* as well as the percentage cover of grasses on 18 February.

On 21 May, I harvested the aboveground portion of the plants from all 110 plots. To examine effects on individual biomass and reproductive performance, I subsampled 10 *Triphysaria, Hypochaeris,* and *Lupinus* individuals randomly from each of the plots in which they occurred. I recorded dry mass and the number of reproductive structures for each of the individually harvested plants. I simply clipped all grasses at ground level without subsampling because the presence of different grass species among blocks complicated comparisons of individual performance. After subsampling individuals, I harvested the remaining vegetation from each plot and recorded total dry mass of parasites and of each host taxon for each plot.

I analyzed mean measures of individual growth and reproductive effort for each plot, as well as total dry mass of each species, using a series of two-way randomized complete block (RCB) ANOVAs. Analyses for each species considered only the relevant subset of the 11 experimental treatments. For example, to examine *Hypochaeris* performance, the four relevant treatments are: *Hypochaeris* alone, with parasites, with grasses, and with both parasites and grasses (Table 1). Thus, for *Hypochaeris,* grass presence and parasite presence are the two main effects of the RCB ANOVA. The analysis for *Lupinus* is similar to that for *Hypochaeris.* For *Triphysaria,* the main effects are presence of grass hosts and presence of a dicot host (either *Hypochaeris* or *Lupinus*). Finally, for grass performance, the main effects are parasite presence and presence of a dicot competitor (either *Hypochaeris* or *Lupinus*). Data were transformed as necessary to satisfy the assumptions of normality and homoscedasticity.

RESULTS

Parasite removals

The total biomass of hosts was significantly larger in removal plots (mean $\pm$ 1 SE = 18.9 $\pm$ 0.9 g) than in control plots (16.6 $\pm$ 0.9 g; $F = 5.20$; df = 1, 20; $P = 0.03$), even though the mass of *Triphysaria* in control plots was small (1.0 $\pm$ 0.1 g). The difference in total host mass can be largely attributed to a 28% increase in the dry mass of the graminoid species in the absence of *Triphysaria* (9.2 $\pm$ 0.9 g) relative to controls (7.2 $\pm$ 0.8 g; $F = 6.14$; df = 1, 20; $P = 0.02$). No other host taxa were significantly affected by the

TABLE 2. The final dry mass of each species in each of the 11 experimental treatments. Values are means ± 1 SE for untransformed data (*n* = 10 for each cell). Ellipses indicate that the species was absent from treatment.

Triphysaria pusilla	Grasses	*Hypochaeris glabra*	*Lupinus nanus*
0.02 ± 0.01	...	...	...
1.8 ± 0.4	7.5 ± 1.1	...	...
0.4 ± 0.2	...	7.0 ± 1.4	...
0.2 ± 0.1	...	...	5.6 ± 1.3
2.2 ± 0.9	7.1 ± 1.5	2.7 ± 0.9	...
1.5 ± 0.4	8.5 ± 1.6	...	1.6 ± 0.7
...	11.8 ± 1.0	...	...
...	...	7.9 ± 1.6	...
...	...	...	4.9 ± 1.6
...	11.4 ± 2.6	3.7 ± 0.7	...
...	9.9 ± 0.9	...	3.7 ± 1.2

parasite removal. The number of host species in removal plots (12.9 ± 0.3) did not differ from that in the controls (12.6 ± 0.4; F = 0.84; df = 1, 20; P = 0.37), and parasite removal did not alter the Shannon-Wiener index of host diversity in any consistent direction (sign test, P = 0.90).

Manipulations of parasites and hosts in 1995

Effect of hosts on parasite performance.—Near the start of the experiment, *Triphysaria* abundance (20.9 ± 2.8 individuals per plot) did not differ among the six treatments that included *Triphysaria* (sampled 18 February, F = 0.75; df = 5, 45; NS). However, by the end of the season, *Triphysaria* performance had been strongly affected by the identity of the available host species (Tables 2,3). *Triphysaria* grown with only grass hosts produced on average 3.2 and 6.4 times more fruits than parasites grown in pure stands of *Hypochaeris* and *Lupinus,* respectively (Fig. 1). One possible explanation for these striking differences in *Triphysaria* performance is that the host taxa may differ in quantity rather than quality, suggesting that larger available host mass might support more parasite growth. Consistent with this idea, plots including *Triphysaria* with only grass hosts contained a slightly larger final host mass

(7.5 ± 1.1 g) than those including *Triphysaria* with only *Hypochaeris* (7.0 ± 1.4 g) or only *Lupinus* hosts (5.6 ± 1.3 g), although these masses were not significantly different (F = 0.62, df = 2, 27; NS). However, differences in host quality remain evident even when the masses of available hosts are accounted for (Table 4), indicating that host identity, rather than host mass, determines *Triphysaria* performance.

Triphysaria performance was exceptionally poor in the absence of hosts, suggesting that *Triphysaria* is largely dependent upon use of a host. For example, on 10 May, of the 10 replicates of the *Triphysaria* without hosts treatment, only three contained any live *Triphysaria,* while *Triphysaria* were still present in 90% of the plots that also included grasses.

Effects of parasitism and competition on host performance.—Near the start of the experiment, the mean cover of grasses (60.2 ± 2.2%) did not differ across the six treatments that included grasses (F = 0.35; df = 5, 45; NS). Similarly, the mean number of *Hypochaeris* (48.8 ± 6.3 individuals per plot) and *Lupinus* (13.4 ± 1.4 individuals per plot) did not differ among those treatments that contained these species (*Hypochaeris*: F = 1.86; df = 3, 27; NS. *Lupinus*: F = 0.62; df = 3, 27; NS).

By harvest, however, grasses had produced substantially more biomass in the absence of *Triphysaria* (Fig. 2). This effect was observed both for grasses grown without competitors and for grasses grown with *Hypochaeris* (post hoc comparisons). Grass biomass was far more affected by the presence of *Triphysaria* than by competition from natural densities of either *Lupinus* or *Hypochaeris* (Fig. 2; Table 5a), even though the biomass of *Triphysaria* (1.8 ± 0.4 g) was only about half that of *Lupinus* (3.7 ± 1.2 g) and *Hypochaeris* (3.7 ± 0.7 g).

In contrast to the grasses, *Hypochaeris* performance was unaffected by parasitism, but was reduced by >50% by competition from natural densities of grasses (Fig. 3a; Tables 2 and 5b). Qualitatively similar effects were observed for all three measures of *Hypochaeris* performance.

TABLE 3. ANOVAs for measures of *Triphysaria* performance with and without different host plants. ''Dicot host'' indicates the presence of either *Hypochaeris* or *Lupinus*.

Source	Total mass			Individual mass			No. fruits per individual	
	df	MS	F	df	MS	F	MS	F
Block	9	0.45	2.63*	9	0.04	6.27***	1.58	7.91***
Grasses	1	8.17	48.10***	1	0.06	8.29**	5.70	28.59***
Dicot host	1	0.01	0.06	1	<0.01	0.44	0.54	2.73
Grass × Dicot host	1	0.34	1.97	1	<0.01	1.18	0.68	3.44
Error	47	0.17		28†	<0.01		0.20	

Notes: All data were log transformed. R^2 = 0.61 for total *Triphysaria* mass per plot; R^2 = 0.71 for individual mass; and R^2 = 0.79 for fruits per individual.

* P < 0.05, ** P < 0.01, *** P < 0.001.

† Reduced degrees of freedom are due to the death of all *Triphysaria* in 19 replicates (7 replicates of *Triphysaria* alone, 5 each of *Triphysaria*–*Hypochaeris* and *Triphysaria*–*Lupinus,* and 1 each of *Triphysaria*–grass–*Hypochaeris* and *Triphysaria*–grass–*Lupinus* treatments).

FIG. 1. Individual performance of *Triphysaria* grown with and without different host plant species. Data are the mean number of fruits produced and the mean dry mass (g) per subsampled *Triphysaria* individual ± 1 SE for untransformed data.
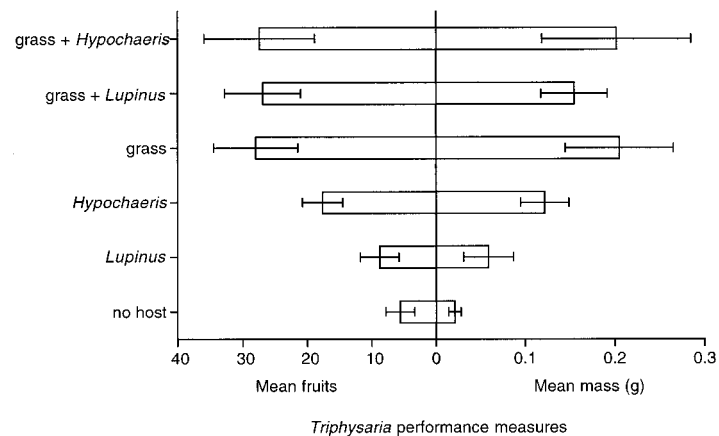
Lupinus performance was similarly unaffected by *Triphysaria* parasitism (Fig. 3b; Tables 2, 5c). Competition from natural densities of grasses significantly reduced total and individual *Lupinus* mass, but had only marginally significant effects on *Lupinus* reproductive performance (Fig. 3b; Table 5c). In addition, there was a significant interaction between the effects of *Triphysaria* and grasses for both reproductive performance and total mass of *Lupinus* (Table 5c), indicating that the combination of parasites and grasses had a more than additive effect in strongly depressing *Lupinus* performance.

DISCUSSION

Effects of hosts on parasite performance

Hosts differed dramatically in suitability for *Triphysaria. Triphysaria* attacking annual grasses were larger and produced more fruits than those attacking either *Lupinus* or *Hypochaeris,* an effect that cannot be explained by the available mass of the different host species. The dramatically improved performance of *Triphysaria* with grasses may be related to the architecture of grass roots. A growing *Triphysaria* root is more likely to contact the highly branched roots of grasses and may be more successful in penetrating these relatively thin roots. For *Triphysaria* seedlings, there may be a premium on quickly finding a host, especially given that many hemiparasites remain small and veg-

etative until successfully attaching to a host (Wilkins 1963, Yeo 1964, Snogerup 1982; M. A. Marvier, *personal observation*).

Triphysaria, like many other generalist root parasites, may attack multiple host individuals simultaneously, and use of multiple hosts can lead to a performance advantage for some parasitic plant species (Marvier 1998). However, in this study, availability of multiple host species did not improve parasite performance beyond that achieved on grasses alone (nonsignificant grass by dicot host interaction). Thus, in the absence of grasses, *Lupinus* and *Hypochaeris* improved parasite performance relative to that of parasites grown with no host, but they appear unimportant for *Triphysaria* growth and reproduction if a grass host is also present.

Effects of parasitism on host performance

Although *Triphysaria* is a small plant, constituting only 5.8% of the total biomass of the control quadrats

TABLE 4. Analysis of covariance of total dry mass of *Triphysaria* in the three treatments that included *Triphysaria* and one host taxa (see Table 1). ''Treatment'' refers to the presence of grasses, *Lupinus,* or *Hypochaeris,* and ''Host mass'' is the dry mass of hosts in each plot.

Source	df	MS	F
Treatment	2	0.47	3.58*
Host mass	1	0.10	0.75
Treatment × Host mass	2	0.01	0.05
Error	24	0.13	

Notes: *Triphysaria* masses were log transformed. $R^2 = 0.56$.
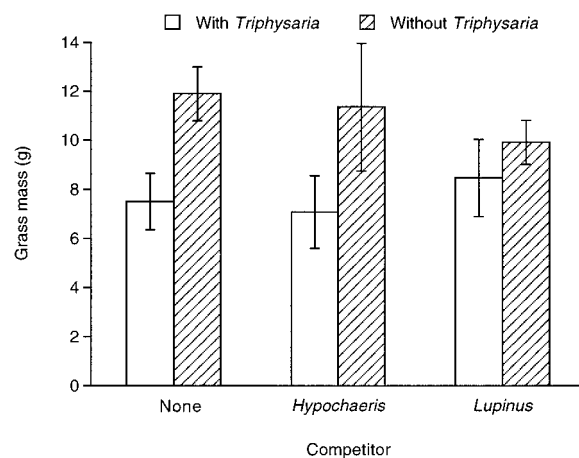* $P < 0.05$.

FIG. 2. Grass performance in different competitive and parasitic environments. Data are the total dry mass (g) ± 1 SE for untransformed data (see Table 2: ''Grasses''). ''None'' indicates grasses grown in the absence of competitors.

TABLE 5. ANOVA results showing responses of host taxa: (a) grasses, (b) *Hypochaeris,* and (c) *Lupinus.*

a) Total dry mass of grasses per plot.‡

Source	df	Total mass MS	Total mass F
Block	9	1.28	3.29**
Parasite	1	5.21	13.43***
Dicot	1	0.17	0.43
Parasite × Dicot	1	0.18	0.46
Error	47	0.39	

b) *Hypochaeris* performance.§

Source	df	Total mass MS	Total mass F	Individual mass MS	Individual mass F	No. inflorescences per individual MS	No. inflorescences per individual F
Block	9	0.69	3.11*	0.05	3.58**	0.22	5.14***
Parasite	1	0.56	2.52	0.004	0.29	0.01	0.33
Grass	1	5.12	23.12***	0.28	20.38***	2.93	68.29***
Parasite × Grass	1	0.30	1.36	0.01	0.74	0.11	2.60
Error	26‖	0.22		0.01		0.04	

c) *Lupinus* performance.¶

Source	df	Total mass MS	Total mass F	Individual mass MS	Individual mass F	No. fruits and flowers per individual MS	No. fruits and flowers per individual F
Block	9	1.24	4.11**	0.25	5.46***	2.09	5.24***
Parasite	1	0.33	1.10	0.05	1.02	1.65	4.12
Grass	1	3.61	11.98**	0.27	5.93*	0.89	2.24†
Parasite × Grass	1	1.54	5.08*	0.18	3.95†	2.70	6.76*
Error	27	0.30		0.05		0.40	

† $P < 0.06$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

‡ ''Dicot'' indicates the presence of either *Hypochaeris* or *Lupinus.* Masses were square-root transformed. $R^2 = 0.48$.

§ $R^2 = 0.66$ for total *Hypochaeris* mass per plot; $R^2 = 0.66$ for individual mass; and $R^2 = 0.81$ for inflorescences per individual. Data were log transformed.

‖ One sample was misplaced.

¶ $R^2 = 0.67$ for total *Lupinus* mass per plot; $R^2 = 0.69$ for individual mass; and $R^2 = 0.69$ for fruits and flowers per individual. Data were log transformed.

in 1994, *Triphysaria* removal significantly affected the host community, reducing total biomass production. Further, *Triphysaria* attack had strongly differing impacts among host taxa. Based on the 1994 findings, I expected the growth of grasses to be far more suppressed by parasitism than that of either *Lupinus* or *Hypochaeris.* Indeed, *Triphysaria* did have its largest effects on grasses in 1995; natural densities of *Triphysaria* significantly reduced the dry mass of annual grasses, while *Lupinus* and *Hypochaeris* were unharmed. While there is some evidence that legumes may generally be preferred hosts of plant parasites (e.g., Gibson and Watkinson 1989, Seel et al. 1993), I found no effect of *Triphysaria* removal on the performance of the most abundant legume, *Lupinus,* in either year (Marvier 1996). Overall, the effects of *Triphysaria* on hosts directly parallel the effects of hosts on *Triphysaria* performance, indicating that the hosts that cause the best parasite performance are also the most harmed by parasitism.

Indirect effects of parasitism: multi-species interactions

In this study, *Triphysaria* performed best on grass hosts, and also exerted its largest effects on this competitively dominant group. Hence, observations of species pairs suggest that *Triphysaria* presence in mixed stands of hosts should lead to the competitive release of dicot hosts. This was not the case; *Triphysaria* did not lead to competitive release of either dicot host species, and, in fact, the combination of *Triphysaria* and grasses led to strongly worsened performance for *Lupinus.* Thus, observations of the direct effects among pairs of species did not lead to correct predictions regarding the outcome of multi-species interactions. Indeed, attempts to extrapolate results from experiments between species pairs to whole communities are frequently unsuccessful (Wootton 1994 and references therein).

The suppression of *Lupinus* by the combination of grasses and *Triphysaria* is most likely due to the increased vigor of individual *Triphysaria* grown with grasses and the spendthrift water use characteristic of most parasitic plants (Press et al. 1988, Press 1989). Grasses support large amounts of *Triphysaria* biomass, and *Triphysaria,* even while suppressing grass growth, uses disproportionately more water than its host species. Thus, after establishing connections with suitable hosts, *Triphysaria* may harm other plant species with-
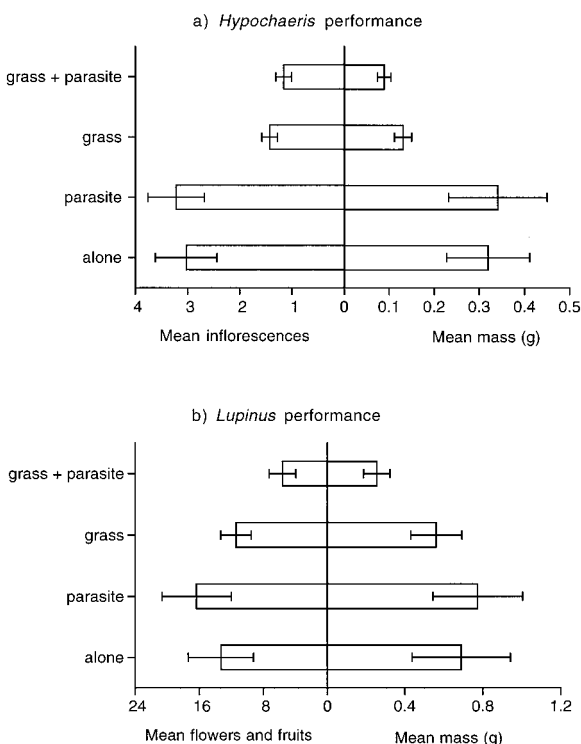
a) *Hypochaeris* performance

b) *Lupinus* performance

FIG. 3. Individual performance of the dicot host species: (a) *Hypochaeris* and (b) *Lupinus.* Bars represent the means for subsampled individuals ± 1 SE for untransformed data.

out actually contacting them, essentially by acting as an aggressive, indirect competitor for soil water. Further, *Triphysaria* individuals attacking grasses were larger, and may have been better able to attack additional host individuals, including nearby dicot species. Regardless of the underlying mechanism, the combination of a plant parasite and its high-quality host caused harm to co-occurring plant species that could not be predicted based on the interactions of species pairs.

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APPENDIX

Species harvested from the coastal prairie community at Bodega Marine Reserve in the 1994 parasite removal study.

Family	Species	Origin	Type
Dicots			
Apiaceae	*Daucus pusillus*	native	annual
Asteraceae	*Achillea millefolium*	native	perennial
	Hypochaeris glabra	introduced	annual
	H. radicata	introduced	perennial
	Madia sativa	introduced	annual
Boraginaceae	*Amsinkia spectabilis*	native	annual
Brassicaceae	*Raphanus sativus*	introduced	annual
Caryophyllaceae	*Cardionema ramosissimum*	native	perennial
	Silene gallica	introduced	annual
	Spergula arvensis	introduced	annual
Fabaceae	*Lupinus nanus*	native	annual
	Trifolium spp.	native	annual
Geraniaceae	*Erodium cicutarium*	introduced	annual
	E. moschatum	introduced	annual
	Geranium molle	introduced	annual
Oxalidaceae	*Oxalis corniculata*	introduced	perennial
Papaveraceae	*Eschscholzia californica*	native	perennial
	Platystemon californicus	native	annual
Plantaginaceae	*Plantago erecta*	native	annual
Polygonaceae	*Rumex acetosella*	introduced	perennial
Portulacaceae	*Calandrinia ciliata*	native	annual
	Claytonia perfoliata	native	annual
Primulaceae	*Anagallis arvensis*	introduced	annual
Scrophulariaceae	*Triphysaria pusilla*†	native	annual
	T. eriantha ssp. *rosea*†	native	annual
Monocots			
Cyperaceae	*Carex* sp.	native	perennial
Juncaceae	*Luzula subsessilis*	native	perennial
Poaceae	*Aira caryophyllea*	introduced	annual
	Avena barbata	introduced	annual
	Bromus diandrus	introduced	annual
	Bromus hordeaceus	introduced	annual
	Elymus sp.	native	perennial
	Lolium perenne	introduced	perennial
	Poa annua	introduced	annual
	Vulpia bromoides	introduced	annual

† Parasite species.