

Linking Parasitic Plant-Induced Host Morphology to Tritrophic Interactions

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ABSTRACT We investigated the tritrophic interactions among southwestern dwarf mistletoe [*Arceuthobium vaginatum* (Willd.) Presl subsp. *cryptopodum*], mistletoe herbivores, and host pine (*Pinus ponderosa* Dougl. ex Laws. and C. Laws. variety *scopulorum* Engelm.)-associated predators. In an observational study, we characterized differences in pine-associated arthropods and pine branch morphology between branches either parasitized by mistletoe (brooms) or not visibly infected. Compared with noninfected branches, brooms had a more reticulate branching structure, collected 36 times more dead needles and supported 1.7 times more arthropod predators. In a manipulative field experiment, we investigated whether pine-associated predators fed upon lepidopteran herbivores of mistletoe and thereby reduced herbivore damage to the parasite. Over a 30-d trial, herbivores fed upon approximately two-thirds of available mistletoe shoots. Predator removal increased herbivore survival by 56% but had no detectable effect on the level of herbivory damage. We speculate that herbivores compete for mistletoe shoots and that increased per-capita feeding compensated for predator reduction of herbivore abundance. In summary, our results demonstrate that mistletoe parasitism altered the pine arthropod community, including an increase in the density of predators that likely feed upon mistletoe herbivores.

KEY WORDS community ecology, detritus, indirect effect, plant morphology, tritrophic

The tritrophic interactions among plants, herbivores, and predators are a topic of long-standing interest in both community and evolutionary ecology (Price et al. 1980). For nearly half a century, it has been recognized that predators can facilitate plant growth from the top-down by protecting plants from their herbivores (Hairston et al. 1960). Plants simultaneously affect predators from the bottom-up (Price et al. 1980). For example, they do so indirectly via their influences on the chemical composition of herbivore tissues (Bowers 2003) and directly by emitting predator-attracting volatiles (Turlings et al. 1990) and by providing the physical habitats in which predators reside (Marquis and Whelan 1996). Disentangling this interplay between top-down and bottom-up interactions is a crucial step toward understanding how consumptive interactions (predation, herbivory, and parasitism) structures ecological communities.

Parasitic plants represent an interesting anomaly to traditional food web models in that they are plants occupying the second trophic level. The suite of herbivores that feed on parasitic plants is typically different from that of their host plant (Mooney 2001, 2003), but parasite

and host plant herbivores most often share a common group of predators (Mooney and Linhart 2006). Some parasitic plants, most notably the dwarf mistletoes (*Arceuthobium* spp.; Viscaceae), alter their host's growth form and other phenotypes (Geils and Hawksworth 2002). Parasitic plants may thus influence predators not only via the paths envisioned by traditional tritrophic models (see above) but also indirectly via their influence on host plant morphology.

Southwestern dwarf mistletoe, *Arceuthobium vaginatum* (Willd.) Presl subsp. *cryptopodum*, is a common and severe parasite of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws. and C. Laws. variety *scopulorum* Engelm., in the Rocky Mountains with well-documented effects on host pine phenotypes, including branch morphology (Hawksworth and Wiens 1996). This parasite is fed upon by several lepidopteran herbivores (Hawksworth and Geils 1996; Mooney 2001, 2003). Using this model system, we asked the following two questions in separate studies: First, are there bottom-up effects of mistletoe on predatory arthropods via parasite-induced changes to host pines? Second, do these pine-associated predatory arthropods prey upon mistletoe herbivores and in doing so reduce mistletoe herbivory?

Materials and Methods

Field Site, Southwestern Dwarf Mistletoe, and Associated Species. Our field sites were at the Manitou Experimental Forest (39° 06' 30" N, 105° 06' 55" W;

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2,400 m), Woodland Park, CO. This site is dominated by ponderosa pine, which is frequently parasitized by southwestern dwarf mistletoe. Like all dwarf mistletoes, southwestern dwarf mistletoe is a shrubby, aerial parasite of conifers (Hawksworth and Wiens 1996). Mistletoe plants are dioecious, with reduced leaves and flowers. Southwestern dwarf mistletoe plants consist of multiple aerial shoots that are 2–5 mm in diameter and commonly grow to 20 cm in height at flowering. Shoots emerge through the pine bark from the parasite's endophytic system embedded in the host's tissues. Shoots persist for several years and perform essentially only a reproductive function of supporting the flowers and fruits. The endophytic system is perennial and serves to parasitize the host by extracting water, minerals, and carbohydrates from the host (Hawksworth and Wiens 1996). Host branches infected with dwarf mistletoes (*Arceuthobium* spp.) develop into a broom-like form characteristic of the mistletoe species and determined by the physiological interaction of host and parasite.

There are nearly 300 species of arthropods associated with the ponderosa pine canopy at Manitou, including >100 species predatory species (Mooney 2006). Spiders (Araneae) and mirids (Miridae: Hemiptera) are the most diverse and abundant predators. Where aphids are abundant, ladybird beetle adults and larvae (Coleoptera: Coccinellidae) as well as lacewing larvae (Neuroptera) are common. Several ants are also common (*Formica* spp.; Hymenoptera: Formicidae) that are predators of many herbivores but are mutualists with some aphids (Mooney and Tillberg 2005, Mooney 2006). Southwestern dwarf mistletoe supports an endemic herbivore fauna (Mooney 2001, 2003). The most abundant herbivores are *Dasypyga alternosquamella* Raganot 1887 and *Promylea lunigerella glendella* Dyar 1906 (Lepidoptera: Pyralidae) caterpillars. These species are closely related and probably sister genera, very similar in size and ecology (Mooney 2003). Their feeding often begins at the shoot base, and even a small amount of herbivore damage kills all distal tissue (K.A.M., personal observations).

Study 1: Parasitism Effects on Host Morphology and Arthropod Communities. In July 2000, we selected 20 mistletoe-parasitized trees. From 10 of these trees (randomly chosen), we selected individual, broomed (parasitized) branches and on the remaining 10 trees, we selected unparasitized (not visibly infected) branches. All branches were 1 to 2 m above the ground and 1.5–3.0 m in length. An infected branch was classified as broomed if its secondary branches formed a reticulate cluster with at least three branchlets crossing and touching each other. This branching morphology was in contrast to the dendritic, nonoverlapping appearance of unparasitized pine branches.

To characterize the differences between broomed and unparasitized branches, we measured a series of morphological variables. Branch length was determined as the distance along an axis from the tree trunk to the farthest branch tip. The distance between two lines parallel to the length axis, touching the left and right flanks of the branch defined branch

width. Likewise, the distance between the highest and lowest tips defined branch height. Other metrics were branch diameter at base, branch age (from count of annual rings), and the fresh masses of foliated branch tips, unfoliated wood, and accumulated detritus (i.e., pine needles). For analysis, we used multivariate analysis of variance (MANOVA) with branch type (broomed, unparasitized) as a predictor variable. Where MANOVAs were significant (here and elsewhere; see below), we examined the analysis of variance (ANOVA) for each dependent variable without adjusting α for multiple comparisons (Johnson 1998). We conducted these analyses with the SAS statistical package (SAS Institute 2001) by using PROC GLM.

The arthropods found on broomed branches included both those associated strictly with the pine host and those strictly associated with the mistletoe; arthropods found on unparasitized branches are just those associated with ponderosa pine. To isolate the indirect effects of mistletoe parasitism on pine arthropods, we removed from our samples the mistletoe plants and discarded the strictly mistletoe-associated arthropods. To collect the remaining, pine-associated arthropods, we beat each branch with a padded stick, thereby dislodging arthropods onto a 2-by-2-m framed sheet. We retrieved each arthropod with a mouth aspirator and deposited it in 70% ethanol. We repeated the collection process (usually three or four cycles), until beating failed to dislodge more arthropods. This methodology, described previously (Mooney and Tillberg 2005), captures most (>97%) arthropods with the exception of adult flies (Diptera) and bees and wasps (Hymenoptera).

We identified all collected pine arthropods to order or family. For analysis, we grouped taxa and functional groups into eight guilds. The three plant-feeding groups were 1) sap-feeding herbivores (*Cinara schwarzii* (Wilson), *Essigella fusca* (Gillette & Palmer), and other aphids; Homoptera: Aphididae, Homoptera) and non-aphid Homoptera (Membracidae and Cicadellidae); 2) chewing herbivores (lepidopteran larvae and Thysanoptera); and 3) detritivores (Psocoptera and Collembola). The five predatory groups were 1) mites (Acari), 2) spiders (Araneae), 3) Hemiptera (principally predatory genera of Miridae); 4) aphid predators (lacewing larvae; Neuroptera) and larval and adult ladybird beetles (Coleoptera: Coccinellidae); and 5) other predators (*Formica* spp. [ants] and pseudoscorpions [Pseudoscorpiones]). These taxonomic groupings doubtlessly mischaracterized the trophic roles of some arthropods. For example, *Formica* ants feed not only as predators but also as herbivores in their capacity as aphid mutualists (Mooney and Tillberg 2005, Mooney 2006), whereas some mites may have been detritivorous or herbivorous. In addition, we have grouped detritivores with herbivores to minimize the number of separate statistical tests performed. Nevertheless, this approach provides a coarse view on how mistletoe parasitism influences pine arthropod communities.

To test for an effect of branch type (broomed or unparasitized) on pine-associated arthropods, we performed separate multivariate analyses of covariance

Table 1. Morphological differences between ponderosa pine branches broomed (parasitized) by southwestern dwarf mistletoe or not infected (unparasitized)

Variable	Branch type		ANOVA tests			
	Unparasitized mean (1 SE)	Broomed mean (1 SE)	df	MS	F	P
Length (m)	1.9 (0.1)	1.7 (0.1)	1,18	0.01	3.63	0.0728
Width (m)	1.8 (0.2)	1.5 (0.1)	1,18	0.37	2.07	0.1678
Height (m)	1.1 (0.1)	1.1 (0.1)	1,18	0.02	0.22	0.6427
Diameter (mm)	54.0 (2.1)	59.0 (2.8)	1,18	124.70	2.02	0.1726
Wood (g)	2,677.5 (442)	4,042.5 (370)	1,18	812.51	6.14	0.0234
Foliage (g)	2,515.3 (544)	1,885 (210)	1,18	0.00	0.1	0.7532
Age (yr)	26 (3.7)	34.5 (2.8)	1,18	361.25	3.35	0.0838
Dead needles (g)	4.6 (4.6)	164.04 (43.5)	1,18	606.65	34.72	0.0001
Branch crosses ^a	0.0 (0.0)	6.3 (0.8)				

MANOVA for all variables significant between branch types. Significant univariate tests in bold.

^a Number of crosses was used as a selection criterion for parasitized branches and is not included in statistical analyses.

(MANCOVAs) for plant-feeding and predatory arthropods. In each analysis, the arthropod groups (three plant-feeding groups and five predatory groups) were multiple dependent variables and branch type was a predictor. In addition, we performed a principal components analysis of the morphological measurements related to branch size (all variables except accumulated detritus and number of crossing branchlets), and we used this component (PC1; see Results) as a covariate in comparisons of arthropod abundance. We followed significant MANCOVAs with individual ANCOVAs. We conducted all analyses with the SAS statistical package (SAS Institute 2001) by using PROC GLM for analysis of covariance (ANCOVA) and MANOVA tests and PROC PRINCOMP for the principal components analysis. We report means and standard errors adjusted for branch size with PC1 score.

Study 2: Effects of Predators on Southwestern Dwarf Mistletoe and Its Herbivores. On 13 August 1999, we selected 20 ponderosa pine brooms (only one per tree) with at least four mistletoe plants each. We chose these parasitized branches (experimental units) to be similar in size and shape. If a branch had more than four mistletoe plants, we completely removed the aerial shoots of all but four plants. We counted the number of shoots of each plant and summed these four subtotals for a total number of shoots per branch. We then randomly selected 10 of these branches for arthropod removal by scouring the foliage and bark with a brush. This treatment thus removed both predators and herbivores. The in situ arthropod community was left intact on the remaining 10 branches. On all 20 branches, we visually inspected the mistletoe plants and removed all larvae. We enclosed all 20 branches within bags of spun-polyester fabric that was both breathable and relatively transparent. We sealed each bag against the base of the branch with wire.

Between 8 and 15 August 1999, we collected mistletoe plants and isolated in excess of 240 third and fourth instars of *D. alternosquamella* and *P. lunigerella*. We kept these larvae in individual petri dishes with fresh mistletoe. On 15 August, we placed 12 larvae on the mistletoe plants of the 10 predator-removal and 10 control branches (a stocking rate of three larvae per

plant). In a previous study (Mooney 2001), the combined abundance of these species was observed as 284 larvae on 112 mistletoe plants or 2.5 larvae per plant. On 15 September, we cut the branches, brought them to the laboratory, and froze them for several days to kill all arthropods. We recorded the number of *D. alternosquamella* and *P. lunigerella* larvae per branch (survival), and we identified and counted other arthropods by taxonomic order. We again counted the number of mistletoe shoots per broom to estimate herbivory.

We had the following a priori predictions for our analyses: 1) predator removal would increase lepidopteran abundance (analyzed as number of larvae per branch); and 2) predator removal would increase mistletoe herbivory (analyzed as number of mistletoe shoots removed). Therefore, we analyzed these data with ANOVA by using one-tailed probability tests (Zar 1999) with PROC GLM (SAS Institute 2001). The distributions of these data approximated a normal distribution and did not require transformation to meet the assumptions of ANOVA (Zar 1999).

Results

Study 1: Parasitism Effects on Host Morphology and Arthropod Communities. Pine branches parasitized by mistletoe displayed a different morphology than unparasitized branches (Table 1). The multivariate comparison (MANOVA) for broomed and unparasitized branches included variables for length, width, height, diameter, age, wood mass, foliage mass, and dead needle mass; the difference was significant (Wilk's lambda = 0.1694, $F = 6.74$; $df = 8, 11$; $P = 0.0025$). Parasitized branches had 150% more wood mass ($P = 0.0234$), 36-fold more dead needle mass ($P < 0.0001$), and were on average shorter ($P = 0.07$) and older ($P = 0.08$) (ANOVAs; Table 1).

The first axis constructed by the principal components analysis (PC1) explained 40% of the multivariate variation and was positively and significantly ($P < 0.05$) correlated with branch length ($r = 0.29$), width ($r = 0.57$), height ($r = 0.35$), wood mass ($r = 0.90$), and foliage mass ($r = 0.65$). Scores for broomed and unparasitized branches did not differ significantly

Table 2. Pine arthropod predator community on ponderosa pine branches broomed (parasitized) by southwestern dwarf mistletoe or not infected (unparasitized)

Arthropod	Branch type		ANCOVA tests				
	Unparasitized mean (1 SE) ^a	Broomed mean (1 SE) ^a	Effect ^b	df	MS	F	P
Acari	1.4 (0.5)	8.1 (2)	Branch	1,16	16.3	17.5	<0.001
			PC1	1,16	1.21	1.3	0.27
			B*PC1	1,16	0.53	0.57	0.46
Araneae	23.2 (5.4)	26.3 (3.8)	Branch	1,16	106.0	1.57	0.23
			PC1	1,16	1924.1	28.51	<0.001
			B*PC1	1,16	12.6	0.19	0.67
Hemiptera	10.6 (2.2)	30.8 (5.8)	Branch	1,16	2112.4	10.1	0.006
			PC1	1,16	144.5	0.69	0.42
			B*PC1	1,16	13.0	0.06	0.81
Aphid predators	5.4 (1.3)	6.8 (1.6)	Branch	1,16	13.0	0.64	0.44
			PC1	1,16	39.3	1.93	0.18
			B*PC1	1,16	25.8	1.27	0.28
Other predators	1.8 (0.6)	2 (0.6)	Branch	1,16	0.04	0.04	0.84
			PC1	1,16	0.44	0.54	0.47
			B*PC1	1,16	0.00	0	0.98
All predators	42.4 (7.5)	74 (10.5)	Branch	1,16	5733.5	9.56	0.007
			PC1	1,16	4671.2	7.79	0.013
			B*PC1	1,16	94.4	0.16	0.70

MANCOVA for all groups significant between branch types. Significant univariate tests in bold.
^a Means and are adjusted for branch size (PC1 score) with ANCOVA.
^b Branch, differences between broomed and unparasitized branches for pine arthropod community. PC1, branch score on principal component analysis factor 1, which is interpreted as a synthetic variable for branch size. B*PC1, interaction between branch type and size.

($F = 0.08$; $df = 1, 18$; $P = 0.77$). Consequently, we took the PC1 score to be a synthetic indicator of branch size, and we used this variable as a covariate in subsequent analyses.

Predator abundance differed between brooms and pine branches not parasitized by mistletoe (Table 2). The multivariate comparison (MANCOVA) by branch type considered abundance of Acari, Araneae, Hemiptera, aphid predators, and other predators; the difference (adjusted for branch size with PC1) was significant (Wilk's lambda = 0.37, $F = 4.16$; $df = 5, 12$; $P = 0.0200$). Compared with unparasitized branches, broomed branches had 580% more mites, 290% more hemipterans, and total predator abundance was increased by 170% (ANCOVAs; Table 2).

The herbivore community did not differ by branch type. The multivariate comparison (MANCOVA) by branch type considered abundance of sap-feeding herbivores, chewing herbivores, and detritivores; the difference (adjusted for branch size with PC1) was not significant (Wilk's lambda = 0.27, $F = 1.15$; $df = 7, 10$; $P = 0.4042$). There was an overall average of 117 (SE = 20) pine herbivores and detritivores per branch. Because of the large increase in detritus on brooms, we performed a separate ANOVA analyzing the effect of branch types on detritivores alone. Although detritivore abundance increased from 22.8 (SE = 5) on control branches to 39.2 (SE = 9) on parasitized branches, this difference was not significant ($F = 2.28$; $df = 1, 18$; $P = 0.15$).

Study 2: Effects of Predators on Southwestern Dwarf Mistletoe and Its Herbivores. After 30 d, we found a mean of 4.4 (SE = 2.3) predators per branch for removal branches and a mean of 18.7 (SE = 3.6) predators per branch for control branches ($F = 9.31$; $df = 1, 18$; $P = 0.0034$). These predators were (by

number) 50% spiders, 14% beetles, and 36% hemipterans. Pine-associated herbivores were relatively rare and did not differ significantly between removal and control branches ($F = 1.28$; $df = 1, 18$; $P = 0.27$). Mistletoe herbivore survival was 56% higher on pred-

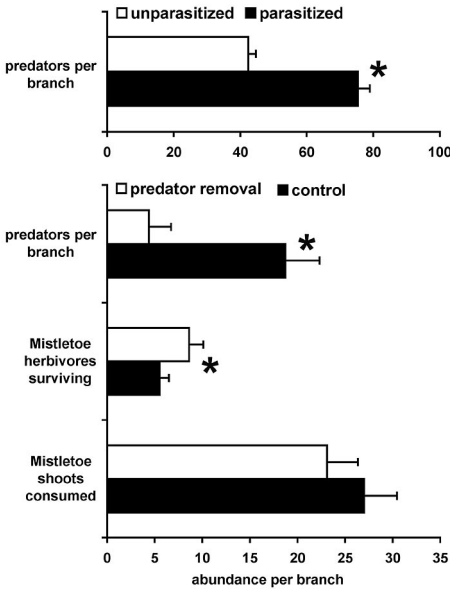


Fig. 1. Differences in arthropod abundance between broomed (parasitized) and unparasitized branches (study 1, top) and predator removal and control branches (study 2, bottom). Mean abundance + 1 SE shown for each variable. Values for predator abundance in study 1 (top) are adjusted means correcting for branch size. Significant differences (*, $P < 0.05$). See Table 2 and text for detailed statistical results.

ator-removal branches ($F = 3.03$; $df = 1, 18$; $P = 0.0494$); 8.6 (SE = 1.5) larvae survived on predator-removal branches (72% survival), whereas only 5.5 (SE = 1.0) larvae survived on control branches (46% survival). The predicted indirect effect of predator removal on herbivore damage to mistletoe was, however, not detected (Fig. 1). The number of mistletoe shoots per pine branch (across both treatments) dropped from 42 (SE = 2.8) at the initiation of the experiment to 25 (SE = 2.4) at its conclusion. For the predator-removal branches (with more herbivores) 23.1 (SE = 3.2) shoots were killed (57% of original shoots). Although 27.0 (SE = 3.4) shoots per branch (67% of original shoots) were killed on control branches (with fewer herbivores), this difference was not significant ($F = 0.68$; $df = 1, 18$; $P = 0.21$).

Discussion

Mistletoe parasitism of pine changed branch morphology from dendritic to reticulate (that is, with numerous crossed branchlets). It was most likely as a result of changes to branch morphology that broomed branches collected 36 times more dead needles than unparasitized branches. Coincident with mistletoe parasitism was a 170% increase in predator abundance. Both broomed and unparasitized branches were selected from heavily parasitized pine trees. Consequently, these results were not attributable to predators and mistletoe coincidentally varying in response to some common pine characteristics.

Our results are consistent with the hypothesis that parasite-induced changes to branch morphology were responsible for the observed effects on predator abundance. In a meta-analysis of 43 studies, Langellotto and Denno (2004) found that increasing habitat complexity with detritus generally increases the abundance of hemipterans and mites. There are several plausible mechanisms for this effect. First, the reticulate branch pattern and accumulation of dead needles creates a microclimatic favorable for these arthropods. Second, increased physical complexity reduces intraguild predation by decreasing encounters among arthropod predators or protecting them from larger insectivorous birds. Regardless of the specific mechanism, our observations supported the notion that parasitism-induced changes in the pine could lead to an increase in arthropod predator abundance.

During our 30-d predator removal experiment, predators significantly reduced the survival of mistletoe lepidopteran herbivores from 72 to 46%. These herbivores consumed or killed nearly two-thirds of the mistletoe shoots. Because mistletoe shoots are essential reproductive structures, such herbivory could substantially reduce mistletoe fitness. However, predator impact on herbivore survival was not accompanied by a change in damage to mistletoe shoots. Both herbivore numbers and individual feeding rates determine the extent of shoot damage. We speculate that high herbivore density in our experiment resulted in competition for limited feeding sites, and that increased per-capita feeding then compensated for reduced her-

bivore survival on branches with predators. Although our stocking rate in 1999 of three larvae per mistletoe plant approximated the density determined that year (2.5 per plant), observations in the three following years suggested that herbivores were unusually abundant in 1999 (K.A.M., personal observation). If we had stocked fewer larvae per branch (as may be more typical), we may have observed a significant, indirect effect of predators on mistletoe.

Parasites of animals frequently change the phenotypes of their hosts in ways that have been demonstrated to be beneficial to the parasite (for review, see Barnard and Behnke 1990, Moore 1995, Moore 2002). Although equivalent studies have not been conducted for parasitic plants, it has been proposed that hosts may serve as extended phenotypes that parasitic plants use to their own reproductive benefit (Tinnin et al. 1982, van Ommen and Whitham 2002). Our results provided equivocal support for the notion that parasitic plants may increase their fitness by using host phenotypes to recruit predators; mistletoe brooming of pine branches increased the density of several groups of arthropod predators, some of which prey upon mistletoe herbivores, but there was no evidence that these predators consequently reduced mistletoe herbivory. Nevertheless, our experiments demonstrated the important consequences of mistletoe parasitism for pine arthropod community structure.

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