

REPORTS

Ecology, 84(4), 2003, pp. 869–874
© 2003 by the Ecological Society of America

FIELD EVIDENCE FOR A RAPIDLY CASCADING UNDERGROUND FOOD WEB

EVAN L. PREISSER¹

Center for Population Biology, 2320 Storer Hall, 1 Shields Avenue, University of California, Davis, California 95616 USA

Abstract. The strength of cascading effects from predators to plants is a controversial issue in work addressing terrestrial trophic interactions. While suppressing herbivores, the effects of some predators dissipate through two trophic levels and only modestly affect land plants. I addressed the strength of the indirect effect of the predatory nematode *Heterorhabditis marelatus* on the bush lupine (*Lupinus arboreus*), where the nematode may protect the plant by killing root-feeding ghost moth (*Hepialus californicus*) caterpillars. I manipulated both predators and herbivores and measured all three components of this cascade in the field. Lupine bushes in eight plots had 24 caterpillars added to each bush's rhizosphere. Four plots had nematode predators added to the soil, while four control plots had no nematodes added. Cascading effects on lupine growth and fitness occurred quickly. The nematode halved herbivore densities in three months, increased lupine trunk growth by 67% within eight months, and increased seed set by 44% in three months. Combined with previous experiments, this result identifies the system as a potent terrestrial trophic cascade. By protecting bush lupine, a nitrogen fixer, this predator may mediate the plant's community effects. Though poorly known, underground predators can have profound effects on terrestrial communities.

Key words: *Hepialus californicus*; *Heterorhabditis marelatus*; *Lupinus arboreus*; predator–prey interactions; soil food web; terrestrial cascade; top-down effects; trophic cascade; underground herbivory.

INTRODUCTION

Trophic cascades, where predators benefit plants by suppressing herbivores, have fascinated ecologists since the Hairston–Smith–Slobodkin “green world” model (Hairston et al. 1960) highlighted the potential impact of indirect trophic effects. Cascades have been found in marine pelagic zones (Estes et al. 1998), freshwater lakes (Carpenter and Kitchell 1993) and rivers (Power 1990), tropical forests (Letourneau and Dyer 1998) and streams (Pringle and Hamazaki 1998), and temperate grasslands (Schmitz 1994). Argument about the usefulness of the cascade “concept” as a model for terrestrial interactions led to several analyses of the strength of cascading terrestrial dynamics (Schmitz et al. 2000, Halaj and Wise 2001). These analyses highlight two issues that, together, underlie much of the current debate over trophic-level regulation of terrestrial systems.

The first of these issues concerns the role of complexity in food web dynamics. Cascades imply that

predators' population-level effects on herbivores are reflected in increased plant performance; omnivory or intra-guild predation may reduce a predator's ability to sufficiently control herbivore populations (Polis and Strong 1996, Polis et al. 2000). Complex interactions between and among trophic levels may also occur more commonly in highly reticulate systems. Simplified agricultural food webs had stronger cascading effects of predators on plant performance than did natural systems (Halaj and Wise 2001). Alternatively, the dynamics of natural terrestrial food webs may simply be slower or less transparent than those of rapidly cycling aquatic or agricultural systems (Holt 2000, Power 2000).

The second issue focuses on the biological “significance” of cascading interactions. Suppressing terrestrial herbivores may reduce herbivory, but statistically significant reductions in damage often produce only minimal increases in plant fitness (Halaj and Wise 2001, but see Schmitz et al. 2000). If decreased plant damage due to terrestrial predators is not reflected in plant fitness, it is reasonable to ask whether the addition of predators makes a difference to plant demography or community structure. Even where cascading dynamics occur in terrestrial systems, they might involve only

Manuscript received 5 July 2002; revised 21 November 2002; accepted 25 November 2002. Corresponding Editor: N. Cappuccino.

¹ E-mail: elpreisser@ucdavis.edu

a small subset of species, rather than predator–herbivore–plant interactions in general (Polis et al. 2000). The proposed dichotomy between species-specific and broader community-level cascades has led to considerable debate (Hairston and Hairston 1997, Holt 2000). A predominance of species-specific interactions suggests that plant communities even in cascading systems may not generally be controlled (through predator effects on plant survival/reproduction) by indirect interactions.

An oft-cited example of a terrestrial trophic cascade is the underground nematode–ghost moth–lupine food chain (Strong et al. 1996b, Hairston and Hairston 1997, Pace et al. 1999). Underground herbivory by root-feeding larvae of the ghost moth *Hepialus californicus* on the bush lupine *Lupinus arboreus* can cause thousands of bushes to die off simultaneously (Strong et al. 1995). Field application of systemic insecticide demonstrated that suppressing underground herbivory on bush lupine over a three-year period caused a cumulative 28% increase in seed set and an 18% increase in survival in protected plants (Maron 1998). The entomopathogenic nematode *Heterorhabditis marelatus* preys on root-feeding larvae of the ghost moth, and high nematode abundance is inversely correlated with ghost moth density (Strong et al. 1996a). Areas with low densities of ghost moth caterpillars had higher lupine survival (Strong 1997), suggesting that the nematode increased lupine survival by suppressing *H. californicus*. In a field experiment isolating the three-species chain in outplanted pots, lupine seedlings with nematodes and ghost moth larvae had much higher survival than seedlings with ghost moth larvae and no nematodes (Strong et al. 1999). Some authors have used this research to exemplify trophic-level regulation (Hairston and Hairston 1997). Others, however, caution that the cascade may be an artefact of removing the three-species chain from the full annual climatic cycle for each component species and from the rest of the food web (Strong 1997), which includes nematode-eating fungi (Jaffee et al. 1996), omnivorous underground predators, and saprophagous species subsisting upon detritus.

The experiment reported here sought to study the nematode–ghost moth–lupine chain under natural conditions, in mature stands of bush lupine, where the natural community would have its maximum effects on the cascade. If the cascade demonstrated in a manipulative experiment using potted seedlings was a function of the three-species chain's removal from the full underground food web, then strong fitness-level effects on plants should be reduced or absent for mature lupines in unmanipulated grasslands. In addition, the strong effects shown in earlier experiments on seedlings may not be representative of effects on mature lupines.

METHODS

Culturing and applying the nematode Heterorhabditis marelatus

The standard technique for censusing and culturing entomopathogenic nematodes uses bait insects such as

“waxworms,” larvae of the wax moth *Galleria mellonella* (Zimmermann 1986). In an effort to include more realism, I applied nematodes using four infected waxworm cadavers per bush rather than spraying the soil with a laboratory-made solution of suspended nematodes. The waxworms were infected by placing them in soil from areas on the Bodega Marine Reserve (BMR; Bodega Bay, California, USA) known to have high *H. marelatus* densities; infected waxworms turn a distinctive brick-orange color and are easily identified. *H. marelatus* juveniles colonize soil when they emerge from a host cadaver. The total number of infective juvenile nematodes emerging from a host cadaver ranges widely, from 100 000 to 1×10^6 (E. L. Preisser and D. Strong, unpublished data). *G. mellonella* larvae are much smaller than late-instar *H. californicus* larvae, and previous surveys of the experimental site found an average of five ghost moth larvae/root infected with *H. marelatus* (Strong et al. 1996b). The nematode treatment densities are therefore similar to those occurring in natural conditions.

Experimental design

The experiment was a fully crossed factorial design: predator (the entomopathogenic nematode *Heterorhabditis marelatus*) and no predator (no *H. marelatus*), crossed with water (supplemental water added twice weekly) and no water (ambient soil moisture). The water/no water factor was examined as part of a separate experiment on the effect of watering on lupines; however, it did not impact the results below and is not further discussed. Two contiguous blocks, each containing all four treatment combinations, were established in a 40 × 13 m area in the coastal grassland at BMR in winter 2001. Lupine bushes in this area had very low ghost moth densities in winter 2001, with a mean of one larvae/bush (E. L. Preisser, unpublished data). This area was sampled at the same time for nematodes using *G. mellonella* as bait insects (Zimmermann 1986), and also had very low nematode densities (1/140 bushes surveyed positive for *H. marelatus* presence). I surveyed all the lupines within the two blocks and selected 40 large, mature lupines/block with similar stem diameters (3.79 ± 0.068 cm [mean ± 1 SE]), no detectable *H. marelatus*, and no ghost moth (*Hepialus californicus*) larvae. While this represents a non-random sample of lupines, it also ensures that the experimental plants experienced the same treatment effects and did not enter the experiment weakened by ghost moth herbivory. Other lupines in contact with the selected experimental lupines were removed to minimize intraspecific competition. Each block was divided into four plots, one plot per treatment combination, for a total of two replicates per treatment combination and eight total replicates. Each of the plots had 10 large, mature lupine bushes. To prevent movement of nematodes between plots during the experiment, plot boundaries were trenched and aluminum flashing

placed around them to a depth of 10 cm below and 4 cm above the ground. Movement of both ghost moths and nematodes between lupines during the dry season is minimal (E. L. Preisser, *personal observation*; D. Strong, *personal communication*).

I applied the *H. marelatus* treatment in May 2001 by enclosing four *H. marelatus*-infected waxworms within a wire-mesh cage (to prevent mammals from eating them) and placing the cage in the soil 3–5 cm deep at the base of each lupine. The no-*H. marelatus* treatment had the same experimental procedure applied, but with waxworms killed by cold.

One week after nematodes were applied to the soil, I added 24 second and third instar ghost moth caterpillars to each lupine rhizosphere, in the soil at the base of the trunk. This larval density of ghost moths was between the “intermediate” and “high” densities of 16.8 ± 5.2 and 37.5 ± 4.1 ghost moth larvae/root noted at BMR (Strong et al. 1995). Since the nematodes had not yet begun emerging from the host when placed in the soil, the nematodes’ survival the week before the ghost moth larvae were added was high. To ensure that at least some of the caterpillars I added survived the transition from the soil to the root, I used second and third instar larvae in the field experiment. Previous observations suggest that at this stage survival would be high enough that at least some of the caterpillars would survive to settle on lupine bushes. The caterpillars were raised from eggs laid in winter 2001 by moths collected at BMR and fed sliced carrots, the standard culture technique for ghost moth caterpillars (Wagner 1985). These caterpillars raised on carrots are roughly the same size as those ghost moth caterpillars raised on lupine root, a more difficult culture technique (D. Strong, *personal communication*). Experimental bushes were not protected from natural ghost moth oviposition, as the netting necessary to prevent egg laying might also have interfered with pollinators and/or the activity of ground-dwelling fauna.

Data collection

I assessed abundance of the ghost moth larvae by counting the number of frass tubes at the base of the trunk of each lupine three months into the experiment. These distinctive tubes, unique to *H. californicus* larvae, are made of frass extruded from the root burrow. The frass tubes have the appearance of sawdust bound into a matrix and plug the hole. Other species do not make frass tubes at BMR since there are virtually no other large root-boring insect species on *L. arboreus* at this site (Strong et al. 1996a). Since ghost moth caterpillars do not share root tunnels (Wagner 1985), frass tubes provide a noninvasive index of larval abundance. There is approximately a 1:1 correspondence between the number of frass tubes found on the root and the number of ghost moth larvae present in the root (J. Havstad, *unpublished data*).

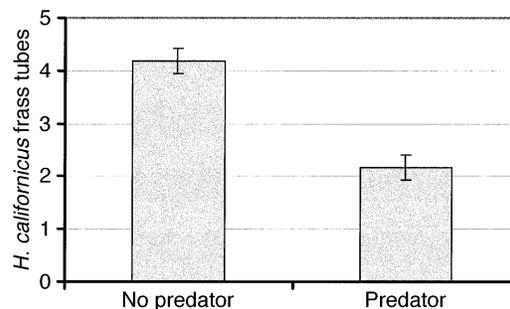


FIG. 1. Number of frass tubes of root-feeding larvae of the ghost moth *Hepialus californicus* in the treatments with the entomopathogenic nematode *Heterorhabditis marelatus* (predator) and without (no predator). The number of frass tubes indicates the number of ghost moth larvae burrowing in the root. Error bars indicate ± 1 SE.

I measured the trunk diameter of each target lupine at the beginning of the experiment and at two, four, and eight months into the experiment. After flowering and seed set three months into the experiment, I counted all of the seedpods on each bush and haphazardly collected 20 pods/bush that were intact and on the verge of dehiscing. I counted all the seeds in these seedpods to determine the number of seeds/seedpod for each bush, and used these data to determine the total number of seeds/bush.

Data analysis

The experiment was analyzed by ANOVA, with predator and block as factors and herbivore density or plant performance as the dependent variable. The indices of plant performance (trunk growth and total seeds/bush) and herbivore density were calculated as the means of 10 mature lupine bushes per plot. Prior to analysis, the data on plant performance and herbivore density were checked for normality. Growth in trunk diameter was expressed as $\ln(\text{basal area})_{\text{current}} - \ln(\text{basal area})_{\text{initial}}$. Repeated-measures ANOVA addressed trunk growth at four and eight months into the experiment. Seed production was analyzed as total seeds/bush (mean seeds/pod \times total seedpods/bush) with initial trunk diameter as a covariate. Because this part of the experiment explicitly planned to test only for the effect of the predator (nematode), statistical tests used the fixed main effect “predator.” The “block” effect was used to control for spatial effects. The statistical package JMP, version 4.0.3 (SAS 2000), was used for all analyses.

RESULTS

Experimental additions of the entomopathogenic nematode *Heterorhabditis marelatus* halved root boring by the ghost moth *Hepialus californicus* (ANOVA, predator: $F_{1,4} = 15.12$, $P < 0.018$; Fig. 1; see Appendix).

Nematode predation on ghost moth larvae led to greater lupine growth. After two months, mean basal

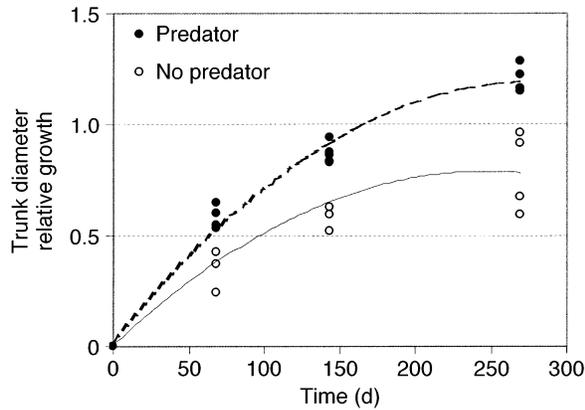


FIG. 2. Basal area (BA) of *L. arboreus* trunks in predator (*H. marelatus*) and no-predator treatments. Trunk diameter relative growth was calculated as $\ln(\text{basal area})_{\text{current}} - \ln(\text{basal area})_{\text{initial}}$. Lines are the best-fit quadratic equation for each treatment (predator line, $r^2 = 0.985$; no predator line, $r^2 = 0.875$).

trunk area in the *H. marelatus* treatment increased 39% more (predator, $8.33 \pm 0.60 \text{ cm}^2$; no predator, $5.99 \pm 1.38 \text{ cm}^2$; means $\pm 1 \text{ SE}$) than those without the nematode. This greater growth rate persisted into the winter, eight months after the start of the experiment, when mean trunk diameter in the predator treatment had grown 67% more (predator, $24.78 \pm 1.56 \text{ cm}^2$; no predator, $14.86 \pm 2.98 \text{ cm}^2$) than in those plots without predators (rm-ANOVA: $F_{1,10} = 88.094$, $P < 0.001$; Fig. 2; see the Appendix).

Nematode predation on ghost moth larvae increased the number of lupine seedpods and seed set. Lupines treated with *H. marelatus* had 30% more seedpods/bush (predator, 451 ± 31 seedpods; no predator, 346 ± 12 seedpods) This led to a 44% increase in total seeds/bush in the predator treatment ($F_{1,3} = 12.15$, $P < 0.040$; Fig. 3; see the Appendix).

DISCUSSION

This research connects all three components of the nematode–ghost moth–lupine food chain in nature with mature plants and extends work done on the three-species cascade in more controlled conditions (Strong et al. 1999) and work with the two-species ghost moth–lupine interaction (Maron 1998, 2001). The nematode had a powerful effect on the ghost moth, demonstrating for the first time that this predator suppresses a root-boring herbivore in mature lupine in nature. The nematode indirectly benefits the bush lupine through its effects on the ghost moth and may cause community-level impacts on coastal grasslands.

Although my experiments have assessed only the short-term impact of the trophic cascade, the predator caused a 39% increase in trunk basal area growth after two months and a 67% increase in growth over eight months. Lupines are long-lived woody perennials, and the cascade may have large cumulative effects on seed

production over a lupine's life-span. The difference in growth was accompanied by a significant increase in the number of seedpods and total seeds/bush. Although *L. arboreus* may be limited by germination sites rather than seed density (Maron and Simms 1997), a 44% increase in mean seed set cannot be dismissed as negligible either demographically or in terms of population effect. This three-species interaction is thus a "species-level cascade" (sensu lato Polis et al. 2000); there may also be community-level effects, but the multiyear time scale of terrestrial interactions makes this difficult to test (Holt 2000).

The indirect interaction between nematodes and lupine bushes occurred within a minimally manipulated soil food web, causing me to reject my initial hypothesis that this cascade would be weakened within the underground food web. The full complement of species-level interactions between underground organisms might have been expected to minimize the cascading trophic effect (Polis and Strong 1996, Polis et al. 2000), but this was not the case. This is significant since the experimental densities of predators and herbivores are comparable to natural conditions. While ghost moth, nematode, and lupine abundance have been cyclic over the past decade (D. Strong and E. L. Preisser, unpublished data), my addition of 24 ghost moth larvae/root was between the "intermediate" and "high" densities of 17 and 38 larvae/root found in 1994 (Strong et al. 1995). When nematodes are found with ghost moths, they often kill a large fraction of the larvae present; a 1995 lupine survey found an average of five larvae/root infected with *H. marelatus* (Strong et al. 1996b). Since I did not monitor the entire soil food web, it is impossible to say that my experiment did not (1) alter components present in unmanipulated systems, or (2) happen to examine the food web at a time when other interacting species were absent. My manipulations were purposefully minimal, however, with predator and herbivore densities comparable to natural levels. In addition, intensive yearly sampling for six years has revealed no other lupine root borers (the vertebrate exception being the pocket gopher, *Thomomys bottae*,

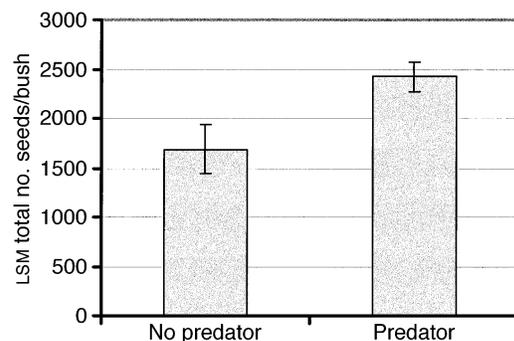


FIG. 3. Total least-square mean seed production of *L. arboreus* bushes in the predator vs. no-predator treatments. Error bars indicate $\pm 1 \text{ SE}$.

which occasionally chews roots of young lupine) present at BMR (D. Strong, *personal communication*).

There are several possible reasons why this system has strongly cascading three-species dynamics. The ghost moth *H. californicus*, vulnerable to a wide range of predators in the detritus, has few predators once it settles within lupines. Only *H. marelatus* and the insect-eating fungus *Beauveria bassiana* cause significant mortality in late-instar larvae, and the larvae have no known parasitoids (Wagner 1985). In the midst of a complex food web, ghost moth larvae in lupines are thus directly affected by only a subset of possible predators. The larvae can be large, and root borers in general have a large per capita effect on plants (Brown and Gange 1990, Pomerinke et al. 1995). By reaming and cutting vascular cells, they destroy root–shoot connections; they may also increase the plant's vulnerability to soil-borne pathogens (Brown and Gange 1990). Maron (1998) found that below-, but not aboveground, herbivory decreased lupine survival, despite the fact that aboveground herbivores were at least an order of magnitude more abundant than belowground ghost moth larvae. In addition, the nematode *H. marelatus* is capable of an extraordinary numerical response to its prey/hosts. The cadavers of even small ghost moth larvae can produce hundreds of thousands of nematodes (E. L. Preisser and D. Strong, *unpublished data*). Mathematical modeling of this nematode–ghost moth interaction indicates that a kill can saturate the rhizosphere with nematodes, leading to the decimation of local prey populations (C. Dugaw, *unpublished manuscript*).

The numerical response of nematode predators to their prey, the paucity of linkages between the root-boring larvae and other predators, and the ghost moth's potent effect on lupines may create a powerfully linear food chain within the larger food web. Underground trophic interactions are often described as complex and interdigitated due to factors like omnivory, size-dependent predation, and spatial heterogeneity (De Ruiter et al. 1995, Polis and Strong 1996). Absent experimental error, my findings support two possible scenarios. First, the underground web may have been suppressed, or highly variable in time and space. If true, then under different circumstances I might have seen attenuation of the predator's trophic signal. The second option is that this is a true food chain, with the three species interacting so strongly with each other, and so little with other organisms, that the trophic-level dynamics characteristic of simplified systems are the most appropriate model (Hairston and Hairston 1997, Halaj and Wise 2001). The nematode specializes on ghost moth larvae, ghost moth larvae specialize on the lupine, and the lupine is particularly vulnerable to root-feeding herbivores. Other organisms from the larger food web (e.g., nematode-trapping fungi, the insect-eating fungus *B. bassiana*, or the tussock moth *Orgyia vetusta*)

may have an impact, but their effect is relatively slight (or present only in some areas, under some conditions).

While unproven, the community-level effects of this interaction could be substantial. Lupines are influential components of coastal vegetation as prodigious nitrogen fixers, and N is released both through leaf detritus and when the plants die. This pulse of N into N-poor grassland soil allows nonnative annuals like *Lolium multiflorum* and *Bromus diandrus* to invade (Maron and Jefferies 1999). With repeated cycles of lupine growth, death, and resprouting, the soils accumulate N and native plants are competitively inferior, favoring the faster growing invaders. By indirectly increasing lupine growth, nematodes increase the amount of N released in the soil, ultimately producing community-level effects. The strength of the nematode–ghost moth–lupine cascade over the short term suggests that this indirect facilitation of lupine growth may be critical to the long-term dynamics of coastal grasslands.

ACKNOWLEDGMENTS

This research would not have been possible without David Spiller and Donald Strong. Tom Schoener, Andrew Sih, David Spiller, and Donald Strong made helpful comments on early drafts of this paper. It was also greatly improved by the comments of Peter Hambäck, and an anonymous reviewer. The Strong lab helped with many phases of this experiment, as did Joyce and Elizabeth Havstad. Funds for this research came from a Mildred Matthias University of California Natural Reserve System grant, Bodega Marine Laboratory Travel Grants, and NSF grant DEB-9508673 to D. Strong. This is contribution #2167 of the Bodega Marine Laboratory, UC Davis.

LITERATURE CITED

- Brown, V., and A. Gange. 1990. Insect herbivory below ground. *Advances in Ecological Research* **20**:1–58.
- Carpenter, S., and J. Kitchell. 1993. The trophic cascade in lakes: synthesis of ecosystem experiments. *Bulletin of the Ecological Society of America* **74**:186–187.
- De Ruiter, P., A. Neutel, and J. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* **269**:1257–1260.
- Estes, J., M. Tinker, T. Williams, and D. Doak. 1998. Killer whale predation on sea otters linking oceanic nearshore ecosystems. *Science* **282**:473–476.
- Hairston, N., and N. Hairston, Sr. 1997. Does food web complexity eliminate trophic-level dynamics? *American Naturalist* **149**:1001–1007.
- Hairston, N., F. Smith, and L. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**:421–425.
- Halaj, J., and D. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? *American Naturalist* **157**:262–281.
- Holt, R. 2000. Trophic cascades in terrestrial ecosystems. Reflections on Polis et al. *Trends in Ecology and Evolution* **15**:444–445.
- Jaffee, B., D. Strong, and A. Muldoon. 1996. Nematode-trapping fungi of a natural shrubland: tests for food chain involvement. *Mycologia* **88**:554–564.
- Letourneau, D., and L. Dyer. 1998. Experimental test in lowland tropical forest shows top-down effects through four trophic levels. *Ecology* **79**:1678–1687.
- Maron, J. 1998. Insect herbivory above- and belowground: individual and joint effects on plant fitness. *Ecology* **79**:1281–1293.

- Maron, J. 2001. Intraspecific competition and subterranean herbivory: individual and interactive effects on bush lupine. *Oikos* **92**:178–186.
- Maron, J., and R. Jefferies. 1999. Bush lupine mortality, altered resource availability, and alternative vegetation states. *Ecology* **80**:443–454.
- Maron, J., and E. Simms. 1997. Effect of seed predation on seed bank size and seedling recruitment of bush lupine (*Lupinus arboreus*). *Oecologia* **111**:76–83.
- Pace, M., J. Cole, S. Carpenter, and J. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* **14**:483–488.
- Polis, G., A. Sears, G. Huxel, D. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology and Evolution* **15**:473–475.
- Polis, G., and D. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.
- Pomerinke, M., D. Thompson, and D. Clason. 1995. Bio-nomics of *Cleonidius trivittatus*: native biological control of purple locoweed. *Environmental Entomology* **24**:1696–1702.
- Power, M. 1990. Effects of fish in river food webs. *Science* **250**:811–814.
- Power, M. 2000. What enables trophic cascades? Commentary on Polis et al. *Trends in Ecology and Evolution* **15**:443–444.
- Pringle, C., and T. Hamazaki. 1998. The role of omnivory in a neotropical stream: separating diurnal and nocturnal effects. *Ecology* **79**:269–280.
- SAS Institute. 2000. JMP start statistics user's manual. Version 4.0.3. Second edition. SAS Institute, Cary, North Carolina, USA.
- Schmitz, O. 1994. Resource edibility and trophic exploitation in an old-field food web. *Proceedings of the National Academy of Sciences of the United States of America* **91**:5364–5367.
- Schmitz, O., P. Hamback, and A. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effect of carnivore removal on plants. *American Naturalist* **155**:141–153.
- Strong, D. 1997. Subterranean insect–plant foodwebs: strange natural enemies and their enemies. *Bulletin of the Ecological Society of America* **78**:36.
- Strong, D., J. Maron, P. Connors, A. Whipple, S. Harrison, and R. Jefferies. 1995. High mortality, fluctuation in numbers, and heavy subterranean insect herbivory in bush lupine, *Lupinus arboreus*. *Oecologia* **104**:85–92.
- Strong, D., A. Whipple, and A. Child. 1996a. Notes from underground: heavy insect herbivory and potent natural enemies. *Bulletin of the Ecological Society of America* **77**:429.
- Strong, D., A. Whipple, A. Child, and B. Dennis. 1999. Model selection for a subterranean trophic cascade: root-feeding caterpillars and entomopathogenic nematodes. *Ecology* **80**:2750–2761.
- Strong, D., A. Whipple, A. Child, S. Kraig, M. Bondonno, K. Dyer, J. Maron, and H. K. Kaya. 1996b. Entomopathogenic nematodes: natural enemies of root-feeding caterpillars on bush lupine. *Oecologia* **108**:167–173.
- Wagner, D. 1985. The biosystematics of *Hepialus* F. s. lato, with special emphasis on the *californicus-hectoides* species group. Dissertation. University of California, Berkeley, California, USA.
- Zimmermann, G. 1986. The “*Galleria* bait method” for detection of entomopathogenic fungi in soil. *Journal of Applied Entomology* **102**:213–215.

APPENDIX

A table with results of ANOVA analysis of (1) frass tubes/bush, (2) trunk diameter relative growth, and (3) total seeds/bush are available in ESA's Electronic Data Archive *Ecological Archives* E084-016-A1.