

## Resource edibility and trophic exploitation in an old-field food web

(herbivory/plant anti-herbivore defense/grasshoppers/spiders/trophic interactions)

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**ABSTRACT** I tested a food web model that predicts how environmental productivity (nutrient supply) and top carnivores should mediate interactions among herbivores, edible plants, and plants that are resistant to herbivory because they possess anti-herbivore defenses. Feeding trials with the dominant grasshopper herbivore at the study site confirmed that certain plant species were resistant to herbivory because of protection by pubescent leaves and stems. Experimental food webs with various numbers of trophic levels composed of edible and resistant plants, grasshoppers, and hunting spiders were assembled in enclosure cages. I randomly assigned half of the cages to a nutrient-enrichment treatment and half remained as a control. Nutrient supply directly enhanced primary productivity and plant and herbivore biomass. Experimentally changing spider abundance caused a classic “trophic cascade” in which herbivore biomass increased and edible plant biomass decreased. Resistant plant biomass increased. These results matched predictions of the model with one exception. A trophic cascade was not observed under enriched conditions. The study nevertheless shows that a simple model attempting to explain heterogeneous interactions in food webs may give considerable insight into the dynamics of natural systems.

Understanding the role of consumers and resources in structuring ecological food webs has been the goal of considerable research (1–3) inspired largely by the seemingly simple question (4), Why is the world green or, more specifically, Why do herbivores seldom overexploit their plant resources? A straightforward answer was presented as part of a hypothesis, known conventionally as HSS (4), that predicts how consumer–resource interactions should structure ecological food webs. HSS proposes that the world is green because herbivore populations are limited by their predators to the extent that they are unable to reach densities sufficient to consume most of the available plant resources. An equally straightforward alternative to HSS (5, 6) proposes that the world is green because many plants are resistant to herbivory because they are nutritionally unacceptable or are protected by plant anti-herbivore defenses. Although there is some support for each alternative (1, 7–11), it is becoming increasingly apparent that the dynamics of natural systems are far more complex than implied by these fairly simple alternatives. This is because species interactions within food webs depend on balances between “top-down” effects of carnivores and “bottom-up” effects of nutrient supply to plants and plant anti-herbivore strategies (2, 12–17). To understand fully the mechanisms producing “green worlds” we must evaluate hypotheses that address a more complex array of food web interactions (3, 18). One particular hypothesis [the edibility hypothesis (13)] combines HSS and its alternative to predict how productivity (nutrient supply) and carnivores mediate interactions among herbivores, edible plants, and resistant plants. I report on experiments that show carnivores

and nutrient supply have strong direct effects on interactions among herbivores and plants in ways that are consistent with the edibility hypothesis. This shows that simple hypotheses of heterogeneous interactions in food webs can give considerable insight into dynamics of complex natural systems.

The edibility hypothesis makes four predictions about the effects of productivity and carnivores on plant–herbivore interactions.

(i) Holding carnivore density constant, effects of increasing productivity on edible and resistant plants are contingent on the consumption rate of resistant plants ( $f_i$ ). (a) If  $f_i$  is near zero, edible plant biomass should remain constant or decrease and resistant plant biomass should increase. (b) If  $f_i$  is large, edible plant biomass should increase and resistant plant biomass should decrease.

(ii) Holding productivity constant, removing carnivores should produce a “trophic cascade (7),” whereby resistant plant and herbivore biomass should increase and edible plant biomass should decrease.

(iii) Holding carnivore biomass constant, herbivore biomass should increase with increasing productivity.

(iv) Holding productivity constant, herbivore biomass should decrease with increasing carnivore biomass.

The edibility hypothesis has had considerable appeal in ecology as a framework for synthesizing patterns in the structure of food webs (18). Yet it remains virtually untested (but see ref. 13). I tested the edibility hypothesis during the summers 1991–1993 as part of a larger study examining herbivore-mediated interactions in a simple old-field plant community near Parry Sound, Ontario, Canada (46°N 80°W). The site was chosen because it is unproductive; it is in the midst of a temperate hardwood forest that had been abandoned from subsistence farming since 1954 and is still in an early to midsuccessional state. Consequently, nutrient manipulations to enhance productivity were expected to be very effective (see below). The site is dominated by perennial dicots and grasses with a mean species richness of  $4.6 \pm 1.1$  per 0.5-m<sup>2</sup> quadrant ( $n = 25$  plots). Dominant species (>2% of biomass in plots) in rank order of abundance are *Hieracium aurantiacum*, *Solidago altissima*, *Phleum pratense*, and *Fragaria canadensis*. The dominant phytophagous herbivores present at the site are the grasshoppers *Melanoplus borealis* and the field katydid *Orchelimum vulgare*. Larger herbivores such as *Microtus pennsylvanicus*, *Lepus americanus*, and *Odocoileus virginianus* appear to have no measurable impact on the plant trophic level as revealed by my field experiments. Specifically, aboveground live plant biomass in enclosure cages containing grasshoppers and lycosid hunting spiders (*Hogna helluo*) near field densities was  $17.8 \pm 1.27$  (SE) ( $n = 8$ ), whereas biomass in adjacent random plots was  $14.8 \pm 1.02$  (SE) ( $n = 8$ ). These differences are not significant ( $t = 1.53$ ;  $df = 14$ ;  $P > 0.07$ ).

All field work was conducted within a time period relevant to the biology of the key players in the food web. The plant species are early season perennials, which dominate the community after the last frost in late May until late July when they begin to senesce. Correspondingly, *M. borealis* nymphs

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emerge in early June, become adults in late June, and begin to die off in early August. The grasshopper nymphs and adults are abundant during the  $\approx 80$ -day temporal window when the key plants are abundant. Moreover, the grasshoppers reproduce once a year, matching the seasonality of the plant species. The field research described below represents a series of short-term studies to determine whether the mechanisms of species interaction predicted by the edibility hypothesis were indeed plausible in the study system. The study involved a series of field and lab experiments conducted in two phases: (i) evaluation of assumptions and (ii) tests of predictions.

It is noteworthy that stems and leaves of *Hieracium* are covered by small hairs called trichomes (9). My studies revealed that trichomes afford *Hieracium* resistance to herbivory. I conducted a nutrient enrichment experiment in 1991 using the four dominant plant species. Standard herbivore enclosure cages (16, 19) were placed over plants growing naturally in the field. Cages were randomly assigned to a control or nutrient enrichment (commercial  $\text{NaNO}_3$  fertilizer supplied in equal amounts once in each of 4 consecutive weeks for a total application rate of  $15 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ). After 50 days, the experiment was terminated and all aboveground green vegetation was clipped at the soil surface, sorted to plant species, and dried at  $60^\circ\text{C}$  for 48 hr. Plant samples were analyzed for solubility in acid/pepsin (an index of fiber digestibility) and nitrogen content using micro-Kjeldahl techniques (an index of nutrient content). *Hieracium* consistently had the highest average nutritional quality (Table 1), so one should expect preferences for it in the absence of defense by trichomes. This is borne out by a series of standard laboratory preference trials (20) conducted in 1992 in which plant material was presented to individual *M. borealis* housed in 1-liter glass jars covered with nylon screening. I presented individuals a choice (i) among *Hieracium* and plant samples without trichomes (*Solidago*, *Phleum*, and *Fragaria*); (ii) between *Hieracium* samples that had the trichomes shaved off with a razor and *Hieracium* samples with trichomes but in which the razor was drawn backwards over the plant material (sham control); and (iii) a sham control of *Hieracium* with trichomes, *Hieracium* with trichomes removed, and a sham control of plant samples without trichomes (*Solidago*, *Phleum*, and *Fragaria*). When shaving trichomes, every effort was made to avoid cutting the plant tissue as this could improve plant palatability independently of removing the defense. If any tissue was penetrated by the razor, the plant sample was discarded. Trial i revealed that individual grasshoppers had a significant preference (Wilcoxon signed ranks test;  $P = 0.047$ ) for plant samples without trichomes (Fig. 1). Trial ii showed that individual grasshoppers preferred (Wilcoxon test;  $P = 0.019$ ) samples of *Hieracium* that had the trichomes removed (Fig. 1). Trial iii revealed that individual grasshoppers preferred (Friedman test;  $P = 0.047$ ) samples of *Hieracium* with the trichomes removed to plant species

Table 1. Digestible nitrogen contents (g of nitrogen per 100 g of plant biomass) of the four dominant plant species at the Parry Sound study site after a 50-day enrichment experiment

	<i>n</i>	Control	Enriched
Edible			
<i>Solidago</i>	8	$0.60 \pm 0.01^*$	$0.80 \pm 0.05^*$
<i>Phleum</i>	8	$0.49 \pm 0.04^\dagger$	$0.84 \pm 0.01$
<i>Fragaria</i>	8	$0.54 \pm 0.03^\dagger$	$0.65 \pm 0.01^\dagger$
Resistant			
<i>Hieracium</i>	8	$0.69 \pm 0.01$	$0.91 \pm 0.01$

Values are means  $\pm$  SE. Probability values are based on Tukey tests within a treatment where comparisons are against *Hieracium*. \* $P < 0.09$ .

$^\dagger 0.01 < P < 0.001$ .

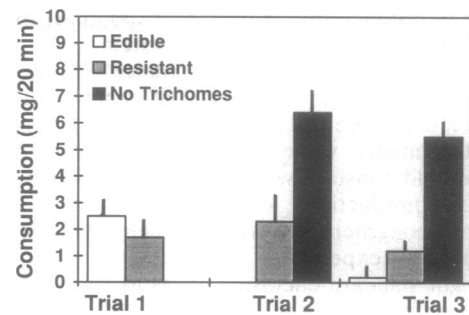


FIG. 1. Consumption of *Hieracium* with trichomes (Resistant), plants without trichomes (Edible), and *Hieracium* with trichomes removed (No Trichomes) by individual grasshoppers. Data are average consumption and associated SEs for  $n = 16$  grasshoppers.

without trichomes and *Hieracium* with trichomes (Fig. 1). Thus, an important basis for grasshopper preferences, beyond nutritional quality, appeared to be the presence or absence of trichomes.

Because nitrogen is likely limiting old-field plant communities (21, 22), I examined the potential for nitrogen competition between edible and resistant plants in 1992 and 1993 by a target-neighbor experiment (23). In such a competition experiment, one observes the growth of a focal individual in the presence of a single conspecific or heterospecific neighbor (treatment) and compares this with the growth of a focal individual without a neighbor (control). Seedlings were transplanted from the field into polystyrene cups containing a 2:1 mixture of sterile potting soil and cleaned sand. Target seedlings were grown individually or with an individual from the other group under ambient light and with unlimited water. I randomly assigned the cups to a nutrient treatment ( $\text{NaNO}_3$  at  $15 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) or a control (no fertilizer). After 6 weeks, the plants were removed from the pots, clipped to separate above- and below-ground parts, and then dried at  $60^\circ\text{C}$  for 48 hr. Aboveground biomass of individual plants was then weighed. There was no significant effect of neighbors on target seedlings in the nutrient control (Fig. 2;  $t$  tests;  $P > 0.25$ ). In the nutrient-enriched treatment (Fig. 2), the presence of neighbors caused a reduction in target seedling growth rate relative to seedlings grown alone (all  $t$  tests;  $P < 0.05$ ). This indicates that edible and resistant plants could be competitors for nitrogen.

Finally, feeding trials with grasshoppers revealed that the consumption rate of resistant plants ( $f_i$ ) was  $0.085 \pm 0.039$  (SE) mg/min ( $n = 16$ ), which was significantly different from 0 ( $t$  test;  $P < 0.025$ ) and it was 55% of the magnitude of consumption rate for edible plants [ $0.152 \pm 0.021$  (SE) mg/min ( $n = 16$ )]. Consequently, prediction *ib*, concerning

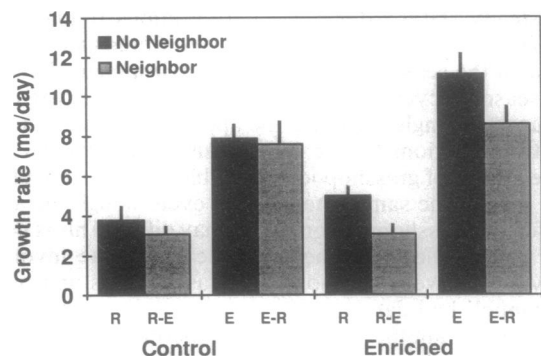


FIG. 2. Means  $\pm$  SE ( $n = 8$ ) in growth rates of resistant (R) and edible (E) seedlings grown alone (No Neighbor) or with a neighbor (Neighbor). R-E (E-R) represents the effect of an edible (resistant) neighbor on a resistant (edible) target.

the effects of productivity on plant biomass in the food web, should be appropriate for this study system.

I tested predictions *ib–iv* during summer 1993 by using an enclosure experiment in the field. The experiment was designed to let herbivore and plant biomass vary in response to different treatments, while productivity and carnivore biomass were held constant within a treatment group. I intentionally fixed productivity levels and carnivore numbers to ensure direct congruence between predictions of the hypothesis and the field experiment.

Forty-eight standard enclosure cages ( $0.1 \text{ m}^2 \times 1 \text{ m}$  high) made of aluminum window screen (16, 19) were arrayed randomly in the field and spaced at  $\approx 1.5\text{-m}$  intervals. I randomly assigned  $\frac{1}{2}$  of all cages to a nutrient treatment ( $\text{NaNO}_3$  at  $15 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ) and  $\frac{1}{2}$  to a control. I assembled three kinds of food webs: (i) plants only; (ii) plants and early-instar grasshopper nymphs; and (iii) plants, grasshopper nymphs, and lycosid hunting spiders. Each type of food web was replicated eight times. Previous experiments (16, 24) suggest that experimental food webs composed of plants, grasshoppers, and spiders are well suited to examine questions about mechanisms of trophic interaction. All animals used in the experiment were caught in the field and were transferred to the cages within 1 hr of capture. I stocked six early-instar *M. borealis* nymphs or six early-instar nymphs and one adult *H. helluo* spider to the cages. The grasshopper numbers were slightly higher than field densities measured during the time of stocking (average, 4.5 nymphs per  $0.1 \text{ m}^2$ ) but spider numbers matched field densities. Initial grasshopper density was intentionally higher to produce a pulse perturbation. This would allow grasshoppers to drift into a steady state with plant biomass, thereby satisfying an important assumption of the hypothesis. Previous experiments (16, 24) have shown that plants and grasshoppers consistently drifted into a steady state following a pulse perturbation in field densities. To verify this, grasshoppers and spiders in each cage were censused every 2 days for the duration of the study. Upon termination of the experiment, all aboveground green vegetation within each cage was clipped at the soil surface, sorted to a functional group, dried at  $60^\circ\text{C}$  for 48 hr, and weighed. Grasshoppers were caught and preserved in 70% alcohol before being weighed.

The experiment was terminated after 35 days (10 June to 15 July) because grasshoppers were molting into adults, and thus the spiders would no longer be effective predators (16, 25). Examining food webs composed of adult grasshoppers would require experiments at a larger scale to accommodate avian predation (25). Thus, the experiment applies specifically to the entire juvenile phase of the grasshoppers. During this phase, grasshopper densities in the cages remained constant for 60% of the time. Other experiments at the study site revealed that grasshoppers in different years tended to reach steady states after pulse perturbations (unpublished data). The exact level of the steady state differed among years because of the seasonal nature of the environment. Because of the seasonal cycle of growth and senescence in the plant community, a single season is the appropriate time frame to evaluate predictions of the hypothesis. Consequently, the relative impact of grasshoppers on edible and resistant plants should remain the same among years even though the absolute effect of grasshoppers on plants may differ. This is borne out by other field experiments at the study site involving two-level food webs composed of grasshoppers and plants only (unpublished data).

I conducted another enrichment experiment, concurrent with the food web experiment, to verify that adding nitrogen enhanced plant productivity. I randomly selected 16  $0.1\text{-m}^2$  plots adjacent to the site used for the food web experiment and clipped the vegetation at the soil surface. I randomly selected 8 plots and applied nitrogen fertilizer ( $15 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ );

the other 8 plots were left as a control. The experiment was terminated after 4 weeks. All aboveground green vegetation was clipped at the soil surface, dried, and weighed. The experiment revealed that total plant production per  $0.1\text{-m}^2$  plot was  $186.4 \pm 13.8$  (SE)  $\text{mg}/\text{day}$  ( $n = 8$ ) in the control plots and  $339.8 \pm 17.0$  (SE)  $\text{mg}/\text{day}$  ( $n = 8$ ) in the enriched plots. This difference was highly significant ( $t$  test;  $P < 0.001$ ).

Consistent with prediction *ib*, edible plant biomass increased with productivity ( $t$  test;  $P < 0.008$ ) and resistant biomass decreased with productivity ( $t$  test;  $P < 0.01$ ) in two-level webs (Fig. 3A). Although the trend in three-level webs was also consistent with prediction *ib* (Fig. 3A), the differences between control and enriched environments were not significant for either edible or resistant plant biomass ( $t$  tests;  $P > 0.25$ ). Consistent with prediction *ii*, the experiment revealed a trophic cascade under control conditions (Fig. 3B). Here, edible plant biomass in two-level webs was significantly lower than in one- or three-level webs (Table 2). Resistant plant biomass was significantly higher in two-level webs than in either one- or three-level webs (Table 2). Prediction *ii* was not supported in the nutrient-enriched treatment (Fig. 3B) as there were no significant differences in edible and resistant plant biomass among the different food webs (Table 2). The effect of productivity on grasshopper biomass was significant ( $t$  test;  $P < 0.05$ ) in two-level webs (Table 3) and marginally significant in three-level webs ( $t$  test;  $P = 0.07$ ) consistent with prediction *iii*. Spiders caused a significant reduction in total grasshopper biomass in cages ( $t$  tests;  $P < 0.05$ ) in both control and nutrient-enriched treatments (Table 3), supporting prediction *iv*.

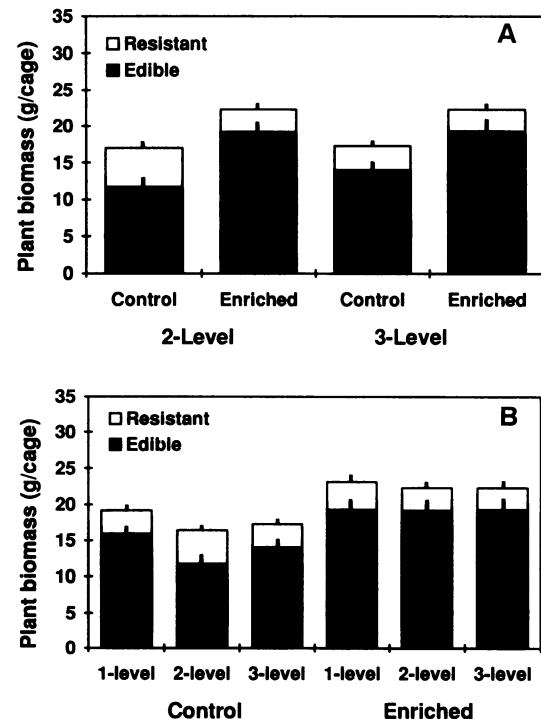


FIG. 3. Means  $\pm$  SE ( $n = 8$  replicates) in effect of nutrient enrichment and carnivores on edible and resistant plant biomass in experimental food webs. (A) Effects of nitrogen on plant biomass, while holding carnivore density constant. In two-level webs (plants and herbivores), nitrogen supply caused an increase in edible plant biomass and a decrease in resistant plant biomass. There was no significant effect of nitrogen supply on plants in three-level webs (plants, herbivores, and carnivores). (B) Plant biomass in food webs with different numbers of trophic levels. Under control conditions, edible plant biomass in two-level webs was lower and resistant plant biomass was significantly higher than in one- or three-level webs. There were no effects in enriched treatments.

Table 2. Probability that mean values are identical in pairwise comparisons of plant biomass in one-trophic level (plants only), two-trophic level (plants and herbivores), and three-trophic level (plants, herbivores, and carnivores) food webs at the Parry Sound field sites.

Pairwise comparison	Plant group	
	Edible	Resistant
Control		
One-level vs. two-level	0.049	0.005
One-level vs. three-level	0.600	0.610
Two-level vs. three-level	0.050	0.041
Nutrient enriched		
One-level vs. two-level	0.958	0.737
One-level vs. three-level	0.970	0.888
Two-level vs. three-level	0.866	0.956

Probability values are calculated by a Tukey test. Tukey tests followed ANOVAs with (2; 21 df) for control and enrichment treatments separately.

The experiment revealed significant top-down effects on food web interactions. Spiders and grasshoppers had a direct influence on adjacent, lower trophic levels and changing spider and herbivore abundance resulted in a trophic cascade (Fig. 3B) in the low productivity treatment. There were also important direct bottom-up effects as increasing nutrient supply resulted in predictable changes in plant biomass in two-level food webs and increases in grasshopper biomass in two- and three-level webs. These results provide encouraging support for the edibility hypothesis.

There was, however, some incongruity between predictions and empirical observations—namely, the lack of a trophic cascade under enriched conditions. This may have happened because nutrient enrichment resulted in a dominant bottom-up effect. Edible plants may have quickly compensated for losses due to herbivory; thus, herbivores were unable to mediate competitive effects between the plant groups. Alternatively, it may have been caused by indirect interactions among nutrient supply, plant defenses, and selective herbivory. Recent studies (26, 27) indicate that the efficacy of a plant defense is conditional and depends on the nutritional quality as well as the physical structure of defended plants relative to undefended plants. Because *Hieracium* consistently had the highest nitrogen content, grasshoppers may have switched preferences for that plant resource as the nutritional profitability outweighed the negative effects of the defense. This, in turn, would reduce the competitive effect of resistant plants on edible plants, which would produce dynamics opposite those predicted by the

Table 3. Total grasshopper biomass (mg per cage) in two types of experimental food web and two nutrient treatments at the Parry Sound study site.

	Two-level web	Three-level web
Control	378.6 ± 18.1	120.4 ± 22.9
Enriched	433.9 ± 24.4	170.0 ± 21.1

Values are means ± SE for  $n = 8$  cages for each treatment–food web combination.

edibility hypothesis. Distinguishing among these explanations will require experiments that explore linkages between physiological and behavioral level processes and food web dynamics (17, 28, 29). The edibility hypothesis offers a promising working foundation to begin understanding the way heterogeneous interactions lead to organizational complexity in natural systems.

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