

Abiotic factors promote plant heterogeneity and influence herbivore performance and mortality in Gambel's oak (*Quercus gambelii*)

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Abstract

Environmental gradients are expected to alter the relative effects of host-plants and natural enemies on phytophagous insects. Moreover, studies of gradients may assist in an identification of the factors important to the outcomes of trophic interactions. We investigated the role of elevation-based variation in environmental conditions (temperature and relative humidity) and foliar nitrogen on tri-trophic interactions in *Quercus gambelii* Nutt. (Fagaceae) during 2001 and 2002. *Quercus gambelii* displayed significant elevational and seasonal fluctuation in foliar nitrogen content, and sites with similar environmental conditions produced similar foliar quality. However, leaf-miners, *Phyllonorycter* spec. (Lepidoptera: Gracillariidae) and *Cameraria* spec. (Lepidoptera: Gracillariidae), did not perform better on trees with a greater nitrogen content. Overall densities of both species declined significantly in 2002, most likely due to severe drought conditions in the south-western USA. Both species exhibited significant, but distinct, patterns in emergence rate with elevation. While environmentally based fluctuation in foliar nitrogen failed to predict the result of trophic interactions, site environmental conditions, as measured by temperature and relative humidity, were strongly related to differences in leaf-miner performance and mortality. The ordination of sites by variation in environmental conditions accurately predicts the relative effect of unexplained vs. natural-enemy sources of mortality for leaf-miners.

Introduction

Recent studies have begun to emphasize the role of biotic and abiotic (environmental) heterogeneity in structuring trophic interactions (Hunter & Price, 1992; Price, 1992; Roininen et al., 1996; Stiling & Rossi, 1997). Abiotic factors, such as inorganic resources and the ambient environment (e.g., water, nutrients, light, temperature), can have significant consequences for natural populations, either directly (Neilson & Wullstein, 1986; Sparks & Ehleringer, 1997; Oleksyn et al., 1998) or indirectly, by altering biotic quality and quantity (e.g., host-plant quality and number, parasite abundance and distribution) (Bryant, 1987; Dudt & Shure, 1994; Reynolds & Crossley, 1997; Moon et al., 2000).

Variation in abiotic and biotic factors may significantly affect the outcomes of trophic interactions by changing the relative importance of bottom-up and top-down effects on insect herbivores (Hunter & Price, 1992). Therefore, studies along natural gradients of abiotic and biotic factors may clarify the role of heterogeneity in determining the strength and direction of trophic interactions in terrestrial ecosystems. To date, few empirical studies have investigated the effects of both abiotic and biotic heterogeneity on the relative roles of bottom-up and top-down control on herbivore populations (Hunter & Price, 1992). Even fewer studies have examined these effects across both spatial and temporal scales (but see Moon et al., 2000; Moon & Stiling, 2003). We know of no studies that have simultaneously examined the role of individual environmental variables in elevational patterns of foliar nitrogen and tri-trophic dynamics.

Elevation gradients consist of several biologically important environmental variables. Temperature (Oleksyn et al.,

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1998), rainfall (Lull & Ellison, 1950), relative humidity (Sparks & Ehleringer, 1997), and nutrient availability (Neilson & Wullstein, 1986; Erelli et al., 1998) vary with elevation. Elevation also may broadly affect herbivore community structure (Janzen, 1973; Hagvar, 1976; Claridge & Singhao, 1978; Fernandes & Lara, 1993) and population dynamics (Whittaker, 1971; Randall, 1982) through a reduction of plant quality (Delucchi, 1958) and number (Janzen, 1973; Randall, 1982). Herbivore diversity (Turner & Broadhead, 1974), parasitism rates (Delucchi, 1958; Whittaker, 1971; Preszler & Boecklen, 1996), and parasitoid abundance (Hagvar, 1976; McCoy, 1990) may also vary with elevation.

Nutrient availability may alter plant nutritive and defense qualities (Clancy, 1992; Koricheva & Haukioja, 1992; Dudd & Shure, 1994; Reed & McCarthy, 1996; Hemming & Lindroth, 1999; Virtanen & Neuvonen, 1999; Lombardero et al., 2000) and potentially affect herbivore preference-performance relationships and parasitism rates (Price, 1992; Kause et al., 1999; Stamp, 2001). The importance of nitrogen balance in plant-insect interactions has long been recognized. Available nitrogen is generally considered to be the nutrient most limiting to insect growth and development (Mattson, 1980; Karowe & Martin, 1989).

Preszler & Boecklen (1996) described the effects of elevation on trophic interactions for *Phyllonorycter* spec. (Lepidoptera: Gracillariidae), a leaf-mining microlepidopteran herbivore, in *Quercus gambelii* (Nutt.) (Fagaceae). The relative importance of top-down and bottom-up forces shifted across an elevation transect, whereby leaf-miner unexplained mortality (host-plant effects) increased and mortality due to parasitism decreased with a gain in elevation. In this paper we assess any possible underlying covariation between shifts in trophic dynamics and the heterogeneity in a set of environmental and biological variables. We measured elevation-based variation in temperature, relative humidity, and foliar nitrogen concentrations, as well as the corresponding performance and mortality for two species of leaf-mining Lepidoptera, *Phyllonorycter* spec. and *Cameraria* spec. (Lepidoptera: Gracillariidae), associated with *Quercus gambelii* in the San Mateo mountain range of west-central New Mexico, USA. Additionally, previously unknown interactions between leaf-mining Lepidoptera and their parasitoids and elevational patterns of foliar nitrogen variation are documented.

Materials and methods

Study system

Quercus gambelii Nutt. (Fagaceae) is a deciduous montane oak associated with ponderosa pine communities of the Southern Rocky Mountains. *Quercus gambelii* occurs at

elevations between 1890 m and 2900 m in central New Mexico. The leaf-mining moths *Phyllonorycter* spec. (Lepidoptera: Gracillariidae) and *Cameraria* spec. (Lepidoptera: Nepticulidae) are common herbivores of *Q. gambelii* (see Aguilar & Boecklen, 1992). *Cameraria* spec. is an upper-surface blotch miner and *Phyllonorycter* spec. a lower-surface blotch miner. Several species of parasitic Hymenoptera (including Ichneumonidae, Chalcidoidea, and Braconidae) are the dominant parasitoids of these leaf-mining herbivores. This group of herbivores and associated parasitoids was chosen due to the confinement within a leaf of their larval stages and the species-specific morphology of their mines. Voucher specimens of *Phyllonorycter* spec. (accession no. 26263) and *Cameraria* spec. (no. 26264) have been deposited in the Arthropod Collection (Museum) at New Mexico State University.

Sampling and data collection

In 2001, an elevation transect was established within Rosedale Canyon on the south-east facing slope of the San Mateo Mountains, Cibola National Forest, in west-central New Mexico, USA. Seven experimental trees were randomly chosen at each of four elevations: E1, 2192 m; E2, 2438 m; E3, 2635 m; and E4, 2866 m. These elevations were chosen to maximize the topographic distribution of *Quercus gambelii* within Rosedale Canyon.

A HoBo® Pro RH/TEMP data logger was placed at a shaded, central location at each site in 2001 and 2002. Daily mean, minimum, and maximum values of relative humidity and temperature were determined, where the 24-h intervals were bracketed by midnight.

Leaf sampling for foliar nitrogen began with the occurrence of first-instar mines of *Phyllonorycter* spec. and *Cameraria* spec., and ended with the pupation of *Phyllonorycter* spec. and *Cameraria* spec. Unmined and undamaged leaves were chosen for leaf nitrogen analysis. At each sampling date, five leaves were randomly sampled from the lower canopy of each tree at each site for foliar nitrogen analyses. Leaves were flash-frozen in the field using liquid nitrogen and subsequently transferred to -80°C and stored until analysis. In 2001, the leaves were sampled on 22 June, 25 July, and 25 September. In 2002, the sampling dates were modified due to severe drought and extensive fire closure of the Cibola National Forest. Leaves were sampled for foliar nitrogen analyses on 24 July and 24 September.

Dumas combustion analysis was used to quantify foliar nitrogen content expressed as percent dry mass. Leaves were dried at 45°C for 48 h and ground to a fine powder. Measurements were carried out at the Laboratory for Environmental Chemistry, INRAM, Las Cruces, NM, USA, using a ThermoFinnigan Flash EA 1112 (CE Elantech, Lakewood, NJ, USA). A NIST (National Institute of Standards

and Technology) peach leaf standard of known nitrogen content was run every 15th sample.

Performance and mortality assays were done for both *Phyllonorycter* spec. and *Cameraria* spec. at each site along the elevation transect. Trees were sampled for leaf-miner densities on 28 September and 6 October 2001, and 4–5 October 2002. Collection date was determined yearly to coincide with *Phyllonorycter* spec. and *Cameraria* spec. pupation. Trees are rarely larger than 4–5 m with open and accessible canopies. As such, most trees were sampled from the ground; larger trees were sampled using a ladder. Each tree was sampled for mined leaves during timed searches of 10 min per tree. For each tree, leaves bearing mines were collected and placed in separate Petri dishes, stored at 20 °C, and monitored for the emergence of leaf-miners or parasitoids. At the conclusion of adult emergence, two measures of performance were determined: percent emergence for each tree and the emergence weight of adult leaf-miners. Leaves with mines that failed were scored for unexplained mortality at sap-feeding (early instar: 1st–2nd instar) or tissue-feeding (late instar: >3rd instar) stages.

Statistical methods

To determine spatio-temporal variation in foliar nitrogen across elevations, a mixed effects repeated-measures analysis of variance (ANOVA) was performed for foliar nitrogen content with elevation (four sites) and sampling date (five dates) as fixed effects, trees nested within sites. The same model, substituting year for sampling date as the time fixed effect, was used to analyze leaf-miner density. *Phyllonorycter* spec. densities were log-transformed (\log_{10} density + 1). Appropriate assumptions of ANOVA (i.e., normality, homogeneity of variance) were examined and met.

Leaf-miner performance measures were characterized using two procedures. First, adult weight (\log_{10} adult weight) was analyzed using analysis of covariance, with sites as groups and tree mean foliar nitrogen and seasonal foliar nitrogen variation (\log_{10} SD) as covariates. Second, leaf-miner emergence across sites for both total mines and late-instar mines was measured using Kruskal–Wallis tests. Developmental success and stage of mortality was examined using contingency table analysis.

To elucidate the temporal importance of foliar nitrogen on leaf-miner performance and mortality, separate linear regressions for leaf-miner density, adult weight, and emergence with mean tree foliar nitrogen were performed according to individual sampling dates.

Step-wise logistic regression was used to analyze parasitoid attack for those mines advancing to late-instar stages. Parasitoids do not attack early sap-feeding instars (R.W. Preszler, pers. comm.). Predictor variables in the full model included elevation, and the average and seasonal variation

of foliar nitrogen for each tree. Contingency table analysis was applied to determine the relative contributions of unexplained mortality (host-plant effects) and parasitism (natural enemy effects) to leaf-miner mortality.

Using weekly average measures of temperature and relative humidity, the characterization of sites by months (June–September) for each year was carried out by principal component analysis on the correlation matrix. Linear regression was performed to determine the relationship between environmental variables averaged across the 7 days prior to each sampling date and foliar nitrogen contents. The average foliar nitrogen content of each site was produced by averaging over trees.

To investigate the relationships between leaf consumption (as a substitute for development time) and foliar nitrogen, Pearson correlations were performed between mine size and foliar nitrogen content for *Phyllonorycter* spec. We chose to focus on mine size as we could not reasonably measure consumption rates or development time in the field. Foliar nitrogen content was averaged over each tree and total mine area (at time of emergence) was determined using the Scion Image® program (Scion Corporation). Due to the coalescence of individual mines prior to emergence, mine size was not measured for *Cameraria* spec.

All analyses were carried out using SAS 8.2 (SAS Institute, Cary, NC) and considered significant at the $\alpha < 0.05$ level. All required post-hoc tests were performed using LSD.

Results

Repeated-measures analysis revealed significant date and seasonal variation by site in foliar nitrogen concentrations (Table 1). Total foliar nitrogen concentrations were consistent with those expected for long-lived trees (Feeny, 1970, 1975; Mattson Jr, 1980). During 2001, foliar nitrogen concentrations differed between all sampling dates and displayed a significant site-by-time interaction while increasing to the highest levels in September (Table 1), which was likely to be due to sampling after the onset of senescence. In 2002, although mean foliar nitrogen did not change between sampling dates, there was an elevation-specific seasonality with a significant increase at E1 and declines at E2 and E4 between July and September (Figure 1; Table 1).

Step-wise linear regressions revealed that in both 2001 and 2002, foliar nitrogen was strongly related to relative humidity (2001: $F_{2,10} = 434.42$, $P < 0.0001$; 2002: $F_{2,6} = 1121.86$, $P < 0.0001$). Temperature was not significantly related to foliar nitrogen and was excluded from subsequent models.

Principal component analysis revealed the first principal axis to explain between 50 and 80% of the total variation.

Table 1 Summary of repeated-measures ANOVA results for foliar nitrogen (percent dry mass) along elevation for 2001 and 2002. Between effects represent results for sites across all dates. Within effects represent results for date and date by site combinations. For date contrasts of effects, mean represents the overall date difference and site represents the site-specific date difference in foliar nitrogen concentration.

Source of variation	Sum of squares	d.f.	Mean square	F	Significance
Between subjects					
Site	0.336	3	0.112	1.32	P = 0.2903
Tree (site)	2.033	24	0.084		
Within subjects					
Date	3.236	4	0.809	29.79	P<0.0001
Date × site	1.226	12	0.102	3.76	P<0.0001
Date × tree (site)	2.607	96	0.027		
Contrast (Effect)	Sum of squares	d.f.	Mean square	F	Significance
June 2001 vs. July 2001					
Mean	0.713	1	0.713	3.53	P = 0.0008
Site	0.035	3	0.011	0.025	P = 0.8626
Tree (site)	1.164	24	0.048		
July 2001 vs. September 2001					
Mean	3.724	1	3.724	143.91	P<0.0001
Site	0.526	3	0.175	6.78	P = 0.0018
Tree (site)	0.621	24	0.025		
July 2002 vs. September 2002					
Mean	0.046	1	0.046	0.88	P = 0.3565
Site	0.994	3	0.331	6.37	P = 0.0025
Tree (site)	1.042	24	0.043		

There was, however, a temporal effect on the first principal component, as the explained variation generally showed a steady decline across months (2001: 60%, 83%, 70%, and 67%, respectively; 2002: 79%, 73%, 58%, and 61%, respectively). Nevertheless, the sites exhibited a consistent ordination along the first principal component. Ordination of sites along the first principal axis according to date was carried out to investigate any grouping patterns (Figures 2 and 3).

Leaf-miners exhibited species-specific patterns of temporal variation, where only *Cameraria* spec. densities were related to sites and only in 2001 ($F_{3,24} = 2.86$, $P = 0.05$). Pair-wise linear contrasts revealed significantly higher *Cameraria* spec. abundances at E1. There were no differences between sites in leaf-miner densities for either species in 2002. Densities decreased significantly for both *Phyllonorycter* spec. and *Cameraria* spec. between 2001 and 2002 (*Phyllonorycter*: $F_{1,27} = 54.59$, $P < 0.0001$; *Cameraria*: $F_{1,27} = 32.67$, $P < 0.0001$).

In 2002, only two leaf-miners survived to adulthood and the overall parasitism rate was below 1%, suggesting wide-scale unexplained mortality. Thus, leaf-miner performance and mortality was not analyzed for the year 2002. The following results pertain only to 2001.

Percentage leaf-miner emergence success was not significantly related to sites for either species (*Cameraria*: Kruskal–Wallis $\chi^2 = 1.61$, d.f. = 3, $P = 0.655$; *Phyllonorycter*:

Kruskal–Wallis $\chi^2 = 3.15$, d.f. = 3, $P = 0.368$), nor did percentage late-instar emergence exhibit differences across sites (*Cameraria*: Kruskal–Wallis $\chi^2 = 0.99$, d.f. = 3, $P = 0.802$; *Phyllonorycter*: Kruskal–Wallis $\chi^2 = 3.05$, d.f. = 3, $P = 0.383$). Developmental success and stage of mortality analysis revealed a strong pattern of emergence rates, with an elevation that contrasted sharply between species (*Phyllonorycter*: Kruskal–Wallis $\chi^2 = 9.34$, d.f. = 3, $P < 0.02$; *Cameraria*: Kruskal–Wallis $\chi^2 = 13.12$, d.f. = 3, $P < 0.004$), where *Phyllonorycter* spec. was most successful at high elevations, while *Cameraria* spec. was successful at low elevations. *Phyllonorycter* spec. displayed no overall or seasonal relationship in adult weight with foliar nitrogen. *Cameraria* spec. did show a marginally significant increase in adult weight with total average nitrogen ($F_{1,50} = 3.49$, $b_1 = 0.55821$, $P = 0.0675$). Mid-summer foliar nitrogen concentration appeared to be most tightly connected to *Cameraria* spec. performance, as the adult weight displayed a positive relationship with nitrogen levels in July ($F_{1,50} = 6.29$, $b_1 = 0.56805$, $P < 0.0154$). This is of note, as late July is probably a very important period in larval development, due to the switch from sap-feeding to tissue-feeding stages (R.W. Preszler, pers. comm.). *Phyllonorycter* spec. mine area was not significantly related to tree foliar nitrogen content ($r_s = 0.002$).

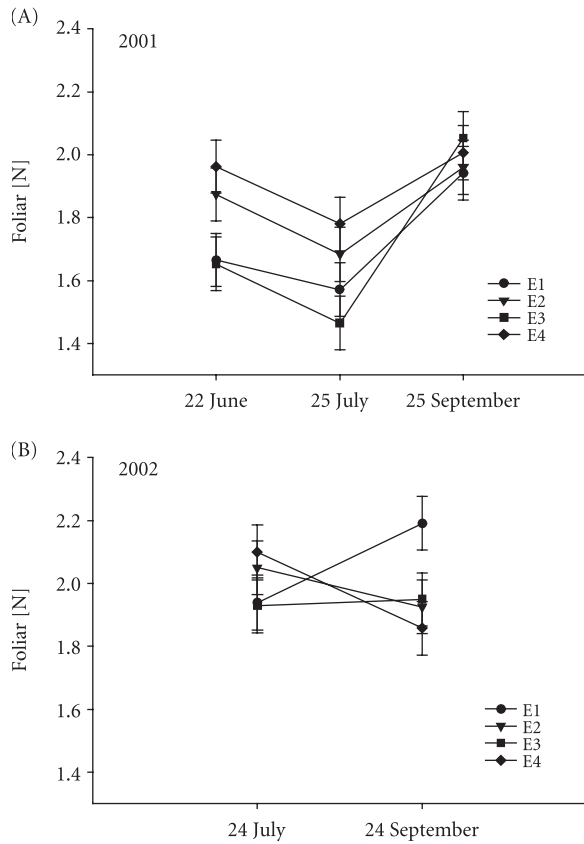


Figure 1 Seasonal variation in foliar nitrogen concentration (percent dry mass) in *Quercus gambelii* according to site. Points represent the least-square mean foliar nitrogen (± 1 SE) of trees within sites. Note that in 2002, June samples were not taken due to fire closure of the national forests in New Mexico.

The low number of trees and parasitism events in this study forced us to group the parasitism and mortality data for *Phyllonorycter* spec. and *Cameraria* spec. Therefore, the following applies only to the leaf-miner feeding guild as a whole. Parasitism rates were found to be significantly related to sites (Wald $\chi^2 = 11.2079$, d.f. = 3, $P = 0.0107$) with the highest levels at sites E1 and E3 (Figure 4). The relative contribution of unexplained mortality (bottom-up effects) and parasitism (top-down effects) were significantly different across sites ($\chi^2 = 14.6612$, d.f. = 3, $P = 0.0021$; Table 2) where parasitism contributed the most to leaf-miner mortality at sites E1 and E3 (Figure 5).

Discussion

Foliar nitrogen concentrations varied significantly across sampling dates and, at times, exhibited site-specific patterns (Table 1; Figure 1). Geographic variation in foliar nitrogen has been explained through concomitant changes

in defense chemistry, abiotic factors, photoinhibition, or allocation to growth and reproduction (Bryant, 1987; Herms & Mattson, 1992; Close & McArthur, 2002), and would be expected to vary with elevation. Here, foliar nitrogen did not exhibit a linear trend across elevation, and suggestions of host suitability patterns influenced strictly by elevation should be taken with caution. Overall concentration and seasonal pattern of foliar nitrogen was unique to sites, whereby those sites closely related in abiotic characteristics also exhibited similar foliar nitrogen levels (Figures 1 and 3). This suggests that foliar nitrogen is correlated with our measured environmental variables (temperature and relative humidity) across the complex topography of the montane environment. Foliar nitrogen has previously been shown to vary with elevation due to changes in gas exchange parameters and vapor pressure gradients (Sparks & Ehleringer, 1997).

Leaf-miner performance was more readily predicted by elevation and environmental variables than by foliar nitrogen. The emergence rate of both species was significantly affected by elevation. Moreover, although *Cameraria* spec. showed a positive response in adult weight to elevated

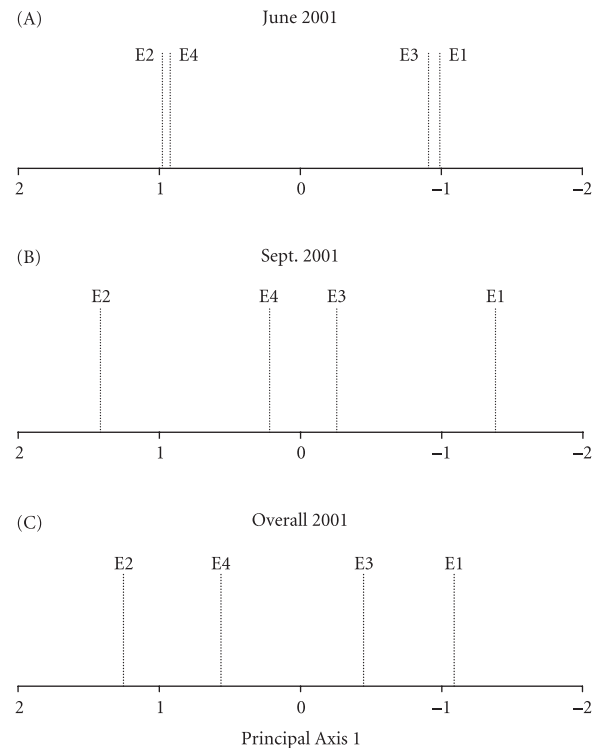


Figure 2 Ordination of sites along the first principal component axis of environmental parameters for each month of the growing season during 2001. Each point represents the first principal component for each site during the respective month. Components were generated using pooled weekly averages of the environmental parameters.

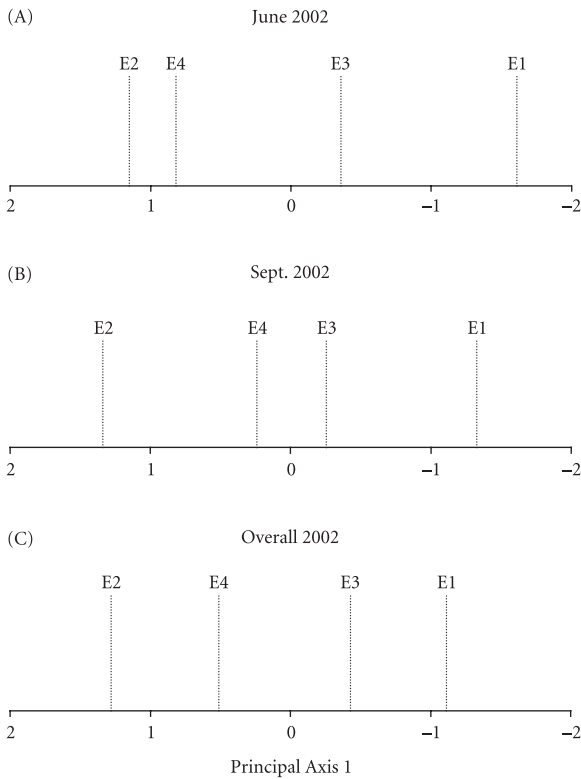


Figure 3 Ordination of sites along the first principal component axis of environmental parameters for each month of the growing season during 2002. Each point represents the first principal component for each site during the respective month. Components were generated using pooled weekly averages of the environmental parameters.

foliar nitrogen, no significant correlation between developmental success and nitrogen was found. Theory predicts that herbivores may respond to nitrogen availability and adjust their rates of consumption accordingly (Mattson Jr, 1980). Importantly, increased feeding time and a subsequent delay in development may leave larvae more vulnerable to predation (Feeny, 1975; Moran & Hamilton, 1980). We found that consumption rates, as measured by mine size at time of emergence, do not vary with foliar nitrogen in *Phyllonorycter* spec. (R.W. Prezler, unpubl.). Nevertheless, total foliar nitrogen may be too crude to determine the precise relationships between insect performance and mortality with foliar nitrogen. Measures of nitrogen quality, such as amino acid content (Karowe & Martin, 1989) and the nitrogen/mineral balance (House, 1969; Clancy, 1992), have been useful in elucidating the influence of nitrogen on herbivores.

In this study, we equate unexplained mortality with host-plant effects. There is substantial evidence that leaf-miners are subjected to fewer diseases than external feeders

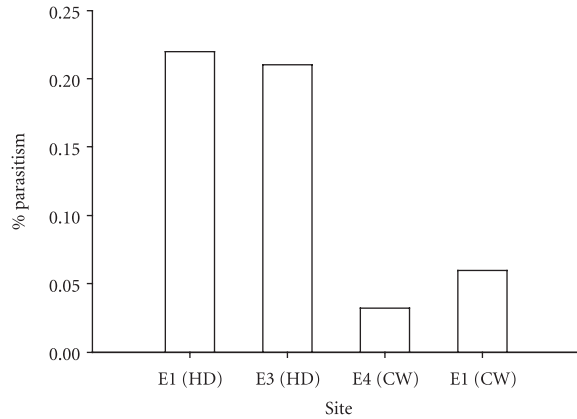


Figure 4 Percent parasitism across sites in 2001. Points represent parasitism rate within sites for all larvae of both leaf-mining species advancing to the third instar. Sites are enumerated by elevation and environmental category in parentheses (HD = hot/dry; CW = cool/wet) and are ordered along the first principal axis of environmental parameters.

(Conner & Taverner, 1997). Additionally, a number of studies on leaf-miners in oaks, including Gambel's oak, document no effect, or even slight positive effects for leaf-miners exposed to plant symbionts (i.e., Prezler et al., 1996b; Faeth & Hammon, 1997) common in the phyllosphere. Competitive effects are also unlikely, as overall and tree-level densities were low and few leaves with multiple mines were observed. This observation is consistent with previous studies from the same system (Prezler & Boecklen, 1996), which have documented a low incidence of multiply mined leaves.

Elevation gradients represent a heterogeneous complex of abiotic factors. Our results suggest that biologically relevant environmental characteristics are highly variable and localized across elevations. Sites within Rosedale Canyon clustered together, based upon local measures of temperature and relative humidity. The ordination of sites

Table 2 χ^2 contingency table for leaf-miner guild mortality source by site: relative rates of parasitism and unexplained mortality. Unidentified sources of mortality are not included in the analysis. Cell values are nested within sites; $\chi^2 = 14.6612$, d.f. = 3, $P = 0.0021$

	E1	E2	E3	E4	Sum
Parasitism					
Number	11	3	15	2	31
% total	5.73	2.40	8.72	1.01	4.51
Unexplained					
Number	181	122	157	196	656
% total	94.27	97.60	91.28	98.99	95.49

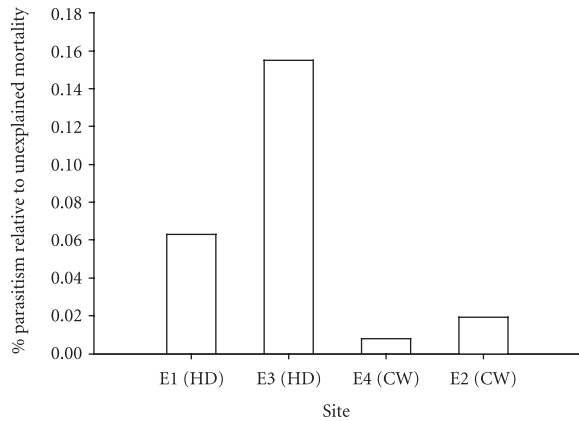


Figure 5 Percent parasitism (top-down effects) relative to unexplained mortality (bottom-up effects) within sites in 2001. Sites are enumerated by elevation and environmental category in parentheses (HD = hot/dry; CW = cool/wet) and are ordered along the first principal axis of environmental parameters.

by environmental parameters results in the same pattern as the variation in trophic relations across sites (Figures 2 and 3). Therefore, local environmental conditions may be important for the determination of the relative strengths and directions of trophic interactions (top-down vs. bottom-up forces), and a detailed knowledge of environmental variability may help to predict the magnitude of those interactions across the landscape. In *Q. gambelii*, warmer, drier sites experienced higher relative parasitism rates, while unexplained mortality was greatest at cool, humid sites (Figure 5).

Temperature and relative humidity may directly affect insect herbivores through the regulation of desiccation regimes and metabolic rates (Andrewartha & Birch, 1954). Although it has been hypothesized that leaf-mining may provide protection from the effects of desiccation and fluctuations in the physical environment (Southwood, 1973; Strong et al., 1984), evidence for such a claim is still equivocal (Conner & Taverner, 1997). Our results for these species of leaf-miners emphasize the need for additional information on the desiccation vulnerability of leaf-mining insects.

The collapse of leaf-miner numbers between 2001 and 2002 and the drastic effects upon leaf-miner development, survival, and parasitoid populations, may be traced to the effects of drought stress (White, 1974; Feeny, 1975; Reese, 1977; Scriber, 1977; White, 1984; Koricheva et al., 1998). A meta-analysis by Koricheva et al. (1998) suggested that herbivores perform poorly on stressed slow-growing plants, such as oaks. In 2002, extreme drought was experienced over much of New Mexico and the timing and amount of summer monsoon precipitation – the predominant source of rainfall for the Chihuahuan desert – was delayed and

reduced. While a yearly fluctuation is common, the extreme reduction in density from 2001 to 2002, dissimilar from previous observations of these same populations (W.J. Boecklen, pers. obs.), suggests that drought may have played a role in reducing leaf-miner abundance.

Our results suggest considerable site-specific variation in both unexplained mortality ('host-plant effects') and natural enemies in leaf-miner populations. The site-specific variation appears to be linked to a corresponding variation of environmental variables acting directly and indirectly on trophic positions. Warmer, drier sites exhibit proportionally higher levels of parasitism (E1 and E3), while cool, humid sites (E2 and E4) experience high levels of unexplained mortality. The relative contributions of top-down (parasitoids) and bottom-up (host-plants) effects for leaf-miner mortality differed by as much as an order of magnitude between sites (Figure 5). Hunter & Price (1992) suggest that environmental variability may determine the outcome of trophic interactions by directly affecting populations, or through the production of heterogeneity in adjacent trophic levels. Our current results are consistent with this view. For *Phyllonorycter* spec. and *Cameraria* spec., environmental variation, as determined by temperature and relative humidity, greatly influences the performance and mortality of immature leaf-miners. Moreover, our results indicate that bottom-up forces determine the strength and importance of natural enemy effects for *Phyllonorycter* spec. and *Cameraria* spec. leaf-miners in *Q. gambelii*.

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