

Elevational and Seasonal Variation in the Foliar Quality and Arthropod Community of *Acer pensylvanicum*

CARALYN B. ZEHNDER,¹ KIRK W. STODOLA,² BLAKE L. JOYCE,³ DAVID EGETTER,³
ROBERT J. COOPER,² AND MARK D. HUNTER⁴

Environ. Entomol. 38(4): 1161–1167 (2009)

ABSTRACT Elevational gradients provide natural experiments for examining how variation in abiotic forces such as nutrient mineralization rates, risk of photodamage, temperature, and precipitation influence plant–insect interactions. At the Coweeta LTER site in the Southern Appalachian Mountains, we examined spatial and temporal variation in striped maple, *Acer pensylvanicum*, foliar quality and associated patterns in the arthropod community. Variation in herbivore densities was associated more strongly with seasonal variation in plant quality than with spatial variation in quality among three sampling sites. Leaf chewer, but not phloem feeder or arthropod predator, densities increased with elevation. Foliar quality, by our measures, decreased throughout the growing season, with decreases in nitrogen concentrations and increases in lignin concentrations. Foliar quality varied among the three sites but not systematically along the elevational gradient. We conclude that, in this system, temporal heterogeneity in plant quality is likely to be more important to insect herbivores than is spatial heterogeneity and that other factors, such as the abiotic environment and natural enemies, likely have substantial effects on herbivore density.

KEY WORDS elevational gradient, herbivory, plant quality, phenolics

Geographic gradients act as natural experiments by providing variation in abiotic factors under which biotic interactions can be evaluated (Yarnes and Boecklen 2005). Elevational gradients provide an excellent example because temperature, soil fertility, risk of photodamage from UVB radiation, and precipitation all vary with changes in altitude (Preszler and Boecklen 1996, Darrow and Bowers 1997). Likewise, a number of plant quality traits change with elevation including foliar nitrogen (Erelli et al. 1998, Hengxiao et al. 1999, Richardson 2004), defensive chemistry such as alkaloids, coumarins, phenolics, and terpenes (Erelli et al. 1998, Hengxiao et al. 1999, Salmore and Hunter 2001, Alonso et al. 2005), structural compounds such as lignin and cellulose (Richardson 2004), and leaf morphology (Hengxiao et al. 1999). These changes in climate and foliar quality associated with elevation will also affect herbivorous arthropods. However, the precise effect that elevation has on plant quality and herbivorous arthropods varies among plant species and arthropod guilds. Consequently, studying these relationships across elevational gradients can help elu-

cidate the relationship among foliar quality, climate, and herbivorous arthropods.

Abiotic factors vary with elevation, and this variation should directly impact herbivores. Temperature generally decreases with increasing elevation and temperature is a major determinant of herbivore growth and development (Simonet et al. 1981, Levesque et al. 2002), movement or activity rates (Wikteliuss 1981), and even distribution (Strathdee et al. 1993, Whittaker and Tribe 1998). Moreover, soil moisture levels differ with respect to elevation because of changes in temperature and precipitation, and soil moisture can affect numerous aspects of an herbivore's life cycle, including emergence and survival (Chen and Shelton 2007, Weston and Desurmont 2008). However, although abiotic conditions differ across elevational gradients, the response of herbivores to variation in elevation is equivocal, with both increases (Bruehlheide and Scheidel 1999) and decreases (Reynolds and Crossley 1997, Suzuki 1998, Hengxiao et al. 1999) in herbivory having been observed with changes in elevation.

Variation in plant quality along an elevational gradient is also expected to influence insect herbivores. Nitrogen is considered the most limiting macronutrient for insect herbivores (Mattson 1980, White 1993). Increases in foliar nitrogen concentrations have been linked with increased insect density, shorter development time, higher survival rates, and higher fecundity (Mattson 1980, Cisneros and Godfrey 2001, Stiling and Moon 2005, Huberty and Denno 2006). In addition to

¹ Corresponding author: Department of Biological and Environmental Sciences, Georgia College & State University, Milledgeville, GA, 31061 (e-mail: caralyn.zehnder@gcsu.edu).

² Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602.

³ Odum School of Ecology, University of Georgia, Athens, GA 30602.

⁴ Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109.

nitrogen, other aspects of plant quality, such as leaf toughness and concentrations of secondary compounds, also influence the performance and behavior of insect herbivores (Abrahamson et al. 2003). Leaves that have high concentrations of cellulose and lignin (i.e., fiber) are stronger, more resistant to damage, and potentially longer lived than leaves with low fiber concentrations (Abrahamson et al. 2003, Richardson 2004). High concentrations of phenolic compounds may deter insect feeding, reduce insect growth and survivorship, and reduce herbivore densities and herbivore species richness (Rossiter 1988, Forkner et al. 2004). Additionally, phenolic compounds can protect leaves from photodamage by acting as antioxidants (Close and McArthur 2002). However, the changes in plant quality with respect to elevation are species specific and still largely unknown.

The purpose of this study was to examine variation in striped maple, *Acer pensylvanicum*, foliar quality along an elevational gradient and to investigate patterns in the arthropod community associated with striped maple. Specifically, we were interested in the influence of foliar nitrogen, phenolics, cellulose, and lignin on arthropod abundance. We predicted that foliar nitrogen concentration would increase with elevation because of associated increases in nitrogen mineralization rates at our study site (Knoepp and Swank 1998). However, because solar and wind stress increase with elevation, we also predicted that percent total phenolics, cellulose, and lignin would increase with elevation. Finally, we predicted that herbivore densities would follow changes in foliar nitrogen, thereby increasing with elevation.

Materials and Methods

Study Site. In February 2005, we established three sites along an elevation gradient, a low elevation site (LOW: 980 m above sea level), a mid elevation site (MID: 1,300 m), and a high elevation site (HIGH: 1,570 m), at the Coweeta Hydrologic Laboratory (hereafter Coweeta). Each site was $\approx 3,000 \text{ m}^2$, and at each site we randomly chose 20 striped maple, *A. pensylvanicum* saplings with an average height of $226.7 \pm 5.8 \text{ cm}$. Coweeta is operated by the U.S. Forest Service and is located in the Nantahala National Forest of western North Carolina (latitude $35^\circ 03' \text{ N}$, longitude $83^\circ 25' \text{ W}$). Mean annual precipitation increases with elevation from 193 cm at low elevation (677 m) to 245 cm at high elevation (1,570 m), and average air temperatures are 3°C lower at high elevation than at low elevation (Swank and Crossley 1988). Rates of nitrogen mineralization increase with elevation (Knoepp and Swank 1998), which seems to generate increases in foliar nitrogen concentrations (A. Ragavendran and M.D.H., unpublished data), but no concomitant increase in plant productivity (Swank and Crossley 1988).

Study Species. Striped maple is a widely distributed, common understory tree found throughout northeastern North America, from Nova Scotia, west to Minnesota and, at higher elevations, as far south as Georgia

(Hibbs et al. 1980). Striped maple rapidly colonizes treefall gaps and forest clear-cuts (Marquis and Passoa 1989). Striped maple is a dioecious species; however, the saplings for this research were prereproductive. Therefore, differences between male and female plants were not examined.

Arthropod Sampling. Budburst phenology is a fundamental driver of arthropod abundance (Hunter 1990) and varies with elevation; therefore, we standardized sampling by budburst date at each site. Specifically, arthropod sampling and leaf quality measurements were made at each site on days 20, 50, 80, and 110 after budburst. We calculated date of budburst for each site by monitoring each tree twice weekly in the beginning of April and averaging the date of budburst at each site. When 50% of buds on a tree had opened, we noted that date as the date of budburst for that tree, and we averaged the date of budburst across all trees at each site. There was an ~ 2 -wk difference between budburst at the low and high elevation sites.

On each sampling date, the entire sapling was non-destructively visually surveyed, and arthropods were counted and categorized into feeding guilds: leaf chewers, phloem feeders, and arthropod predators. Leaf chewers were predominantly free-living Lepidoptera larvae. Leaf rollers, leaf tiers, leaf miners, sawflies, coleopterans, and gall-forming insects were at low densities or absent and are not considered here. Phloem feeders were predominantly aphids, which were not tended by ants. Arthropod predators were predominantly spiders, but also included Reduviidae, Syrphidae, and Coccinellidae.

Plant Quality Estimates. Two haphazardly chosen fully expanded leaves were collected from each tree on each sampling date for plant quality estimates. Striped maples have a single flush of leaves in the spring, so leaf age within an individual tree is homogeneous. Leaves were collected from both terminal and nonterminal branch positions. Although collecting additional leaves would have given us a more representative sample, collecting multiple leaves per sampling date would have potentially damaged some of the smaller saplings. Therefore, we assume that our two leaf sample gives a reasonable estimate of sapling foliar quality. We collected leaf samples immediately after arthropod surveys using scissors to clip each leaf above the petiole.

One leaf was immediately placed into a vial containing 70/30 acetone/water with 1 mM ascorbic acid. This leaf was used to generate the "bulk" standard for the total phenolic assay (below). While in the field, a 6-mm-diameter hole-punch was used to remove two disks of leaf tissue from the other leaf. Disks were punched opposite each other $\approx 3 \text{ cm}$ from the midvein in the middle of the leaf. One disk was used to obtain disk dry weight. The other disk was placed into a 2-ml tube containing 70/30 acetone/water with 1 mM ascorbic acid and used for subsequent phenolic analysis. The leaves and leaf disks collected in the acetone/water solutions were kept on ice. For C:N and fiber analyses, the remainder of the leaf was dried at 64°C in a drying oven and ground into a fine

powder using a ball mill grinder (Spex Certiprep, Metuchen, NJ). The leaf disk used for obtaining dry weight was also oven dried.

Ground leaf samples were used for analysis of C:N ratios and for foliar concentrations of cellulose, hemicelluloses, and lignin. For C:N analysis, ground samples were weighed into tin capsules with a Mettler UMT2 microbalance (Mettler Toledo, Greifensee, Switzerland) and analyzed with a Carlo Erba NA 1500 CHN analyzer (Carlo Erba, Milan, Italy). The remainder of the ground sample was used to measure foliar concentrations of cellulose, hemicellulose, and lignin. Fiber analysis (neutral detergent fiber [NDF], acid detergent fiber [ADF], and lignin) was conducted following the sequential nylon bag procedure (Abrahamson et al. 2003) using an Ankom fiber analyzer (Ankom Technology, Fairport, NY). Hemicellulose was calculated as NDF minus ADF, and cellulose was calculated as ADF minus lignin.

Total phenolic concentrations were measured from the leaf disks collected into 70% acetone using the Folin-Denis assay as described in Hall et al. (2005). Standards for phenolic analysis were generated by multiple sequential extractions of bulk samples in 70% acetone. Bulk samples were generated independently for each site and sampling date by collecting one leaf from each tree at each site on each date (Hall et al. 2005). Phenolic assays produced colorimetric readings that were quantified by using a Bio-Rad microplate reader (Bio-Rad Laboratories, Hercules, CA). Concentrations were obtained by dividing the estimated phenolic quantity by the weight of the dried leaf disk.

Statistical Analysis. To examine spatial and temporal variation in plant quality and insect density, the repeated-measures framework of PROC MIXED with a type I autoregressive model (SAS version 8.2 for Windows) was used with site as the class variable (Littell et al. 1998). To meet the assumptions of normality, all insect densities were $\ln(x + 1)$ transformed. Total phenolics, hemicellulose, cellulose, lignin, and nitrogen concentrations were arcsine square-root transformed.

Additionally, we were interested in examining relationships between the plant quality traits we measured and the likelihood of herbivores presence. Logistic regression analyses (PROC LOGISTIC) were run separately for each of the four dates for both leaf chewers and phloem feeders. Individual trees were replicates, and all three sites were included in each analysis (i.e., 30 trees per analysis). We chose a logistic regression approach because herbivore densities were generally low and particular guilds were often absent from individual saplings. Individual trees were scored as one for herbivore presence or 0 for absence. We tested for multicollinearity among our predictor variables using PROC REG. Subsequently, percent hemicellulose was dropped from all logistic regression analyses because it was highly correlated with other variables (Allison 1999).

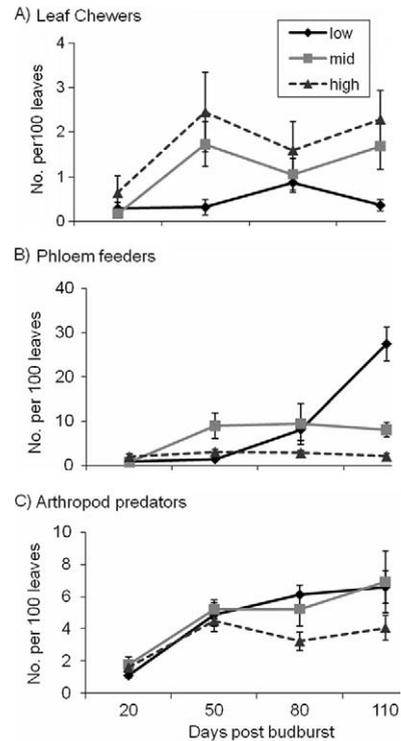


Fig. 1. (A) Leaf chewer, (B) phloem feeder, and (C) arthropod predator densities on striped maple (*A. pensylvanicum*) throughout summer 2005 among three elevations (low: solid black line with diamonds, mid: dashed black line with squares and high: dashed gray line with triangles). Each point is the mean of 20 saplings (\pm SE).

Results

Leaf chewers exhibited the predicted increase in density with elevation (Fig. 1A). Although there were fluctuations in their density throughout the growing season, the LOW elevation site always had the lowest density and the HIGH elevation site always had the highest density (site: $F = 5.65$, $df = 2,57$; $P = 0.006$; date: $F = 4.47$, $df = 3,171$; $P = 0.005$; site \times date: $F = 1.11$, $df = 6,171$; $P = 0.356$). Phloem feeder density was consistently low at the HIGH and MID elevation sites, and phloem feeders exhibited exponential growth over the summer at the LOW elevation site (Fig. 1B; site: $F = 13.08$, $df = 2,57$; $P < 0.001$; date: $F = 45.46$, $df = 3,171$; $P < 0.001$; site \times date: $F = 23.98$, $df = 6,171$; $P < 0.001$). Arthropod predator density increased over the course of the growing season, and there was a greater number of predators at the LOW and MID elevation sites than at the HIGH elevation site (Fig. 1C; site: $F = 5.45$, $df = 2,57$; $P = 0.007$; date: $F = 27.13$, $df = 3,171$; $P < 0.001$; site \times date: $F = 2.26$, $df = 6,171$; $P = 0.040$).

Foliar nitrogen concentrations were highest at the earliest sampling date, and concentrations dropped as the season progressed. At the first sampling date, the LOW elevation site had the highest nitrogen concentrations, with the MID and HIGH elevation sites exhibiting higher nitrogen levels later in the year (Fig.

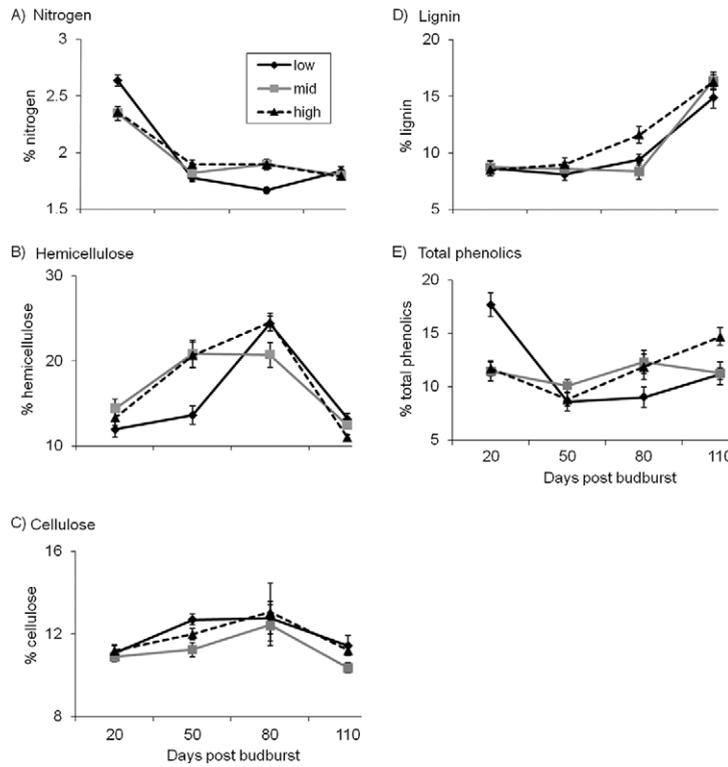


Fig. 2. Striped maple (*A. pensylvanicum*) (A) foliar nitrogen, (B) hemicellulose, (C) cellulose, (D) lignin, and (E) total phenolic concentrations throughout summer 2005 among three elevations (low: solid black line with diamonds, mid: dashed black line with squares and high: dashed gray line with triangles). Each point is the mean of 20 saplings (\pm SE).

2A; site: $F = 0.16$, $df = 2,57$; $P = 0.849$; date: $F = 463.95$, $df = 3,164$ $P < 0.001$; site \times date: $F = 31.44$, $df = 6,164$; $P < 0.001$). Percent hemicellulose increased until the third sampling date, and fell during the final sampling period. Additionally, hemicellulose concentrations varied among sites but not consistently with elevation, and the among-site variation changed over time (Fig. 2B; site: $F = 2.45$, $df = 2,57$; $P = 0.095$; date: $F = 67.09$, $df = 3,163$; $P < 0.001$; site \times date: $F = 6.96$, $df = 6,163$; $P < 0.001$). Percent cellulose was lowest at the first and last sampling date, and there was little variation among sites (Fig. 2C; site: $F = 2.06$, $df = 2,57$; $P = 0.137$; date: $F = 4.50$, $df = 3,163$; $P = 0.005$; site \times date: $F = 0.24$, $df = 6,163$; $P = 0.961$). Lignin concentrations increased over the summer at all three sites (Fig. 2D; site: $F = 1.05$, $df = 2,57$; $P = 0.355$, date: $F = 69.15$, $df =$

3,163; $P < 0.001$; site \times date: $F = 1.22$, $df = 6,163$; $P = 0.299$). Phenolic concentrations were highest at the LOW elevation site on the first sampling date, constant over time at the MID elevation site, and increased at the end of the growing season at the HIGH elevation site (Fig. 2E; site: $F = 0.38$, $df = 2,57$; $P = 0.683$, date: $F = 20.46$, $df = 3,166$; $P < 0.001$, site \times date: $F = 9.53$, $df = 6,166$; $P < 0.001$).

During the early season, trees with high foliar nitrogen concentrations were more likely to host leaf chewers on them (Table 1). During the mid-season, trees with high foliar cellulose concentrations were less likely to host phloem feeders on them (Table 2). However, there were no consistent, season-long patterns among any of the plant quality traits measured and either leaf chewer or phloem feeder density.

Table 1. Parameter estimates (SE) from logistic regression models of the presence of Lepidoptera larvae with plant quality traits (percent cellulose, lignin, nitrogen, and phenolics)

Parameter	Day 20	Day 50	Day 80	Day 110
Cellulose	37.3 (23.1)	-29.5 (19.2)	1.3 (3.9)	-1.15 (12.2)
Lignin	8.6 (9.9)	7.9 (9.6)	-0.3 (3.9)	-3.2 (6.2)
Nitrogen	89.2 (43.1)	54.3 (53.5)	52.0 (41.5)	69.1 (49.7)
Phenolics	-7.1 (5.7)	8.8 (6.8)	-3.05 (4.1)	0.85 (5.5)

Day refers to the no. of days after budburst. Parameter estimates in bold are significant at the $P < 0.05$ level.

Table 2. Parameter estimates (SE) from logistic regression models of phloem feeders presence on plant quality traits (percent cellulose, lignin, nitrogen, and phenolics)

Parameter	Day 20	Day 50	Day 80	Day 110
Cellulose	1.1 (12.9)	-49.4 (23.3)	2.5 (6.1)	-4.1 (16.3)
Lignin	0.4 (6.8)	7.3 (10.9)	4.6 (6.0)	-10.7 (9.1)
Nitrogen	45.5 (32.9)	-14.9 (66.3)	-56.5 (65.8)	27.5 (62.7)
Phenolics	-1.3 (4.2)	-2.1 (7.4)	7.0 (7.1)	-9.21 (6.87)

Day refers to the no. of days after budburst. Parameter estimates in bold are significant at the $P < 0.05$ level.

Discussion

On striped maple, leaf chewer density increased along the elevational gradient, but similar patterns were not observed for phloem feeders or arthropod predators (Fig. 1). Plant quality changed throughout the growing season, but not consistently along the elevational gradient (Fig. 2). Leaf chewers were more abundant on trees with high foliar nitrogen concentrations in the early season, and phloem feeders were less abundant on trees with high cellulose concentrations during the middle of the summer. However, none of the plant quality traits measured was consistently related to herbivore abundance (Tables 1 and 2).

Throughout the 2005 growing season, there were higher caterpillar densities at the HIGH elevation site than at the LOW elevation site. Obviously, leaf chewer densities are responding to more than just variation in plant quality. Interestingly, arthropod predator density was highest at the site with the lowest leaf chewer density, so increased pressure from natural enemies may help explain the gradient in leaf chewer density. Additionally, parasitoids, pathogens, competition with other herbivores, bird predation, temperature, and moisture are all important variables that can vary spatially and influence the abundance of herbivores (Ritchie 2000, Barbosa and Caldas 2007, Kaplan and Denno 2007). Haukioja et al. (1985) observed a similar pattern on mountain birch, and leaf chewer but not phloem feeder or arthropod predator densities increased with elevation, and neither foliar nitrogen nor phenolic concentrations explained herbivore abundance patterns.

Phloem feeders exhibited exponential growth at the LOW elevation site (Fig. 2B). This is most likely because of warmer temperatures at the LOW elevation site that increase population growth rates for phloem feeders such as aphids (Agrawal et al. 2004). High foliar cellulose concentrations corresponded to a reduced probability of hosting phloem feeders. High cellulose and lignin concentrations correspond to tougher leaves, which would be predicted to influence leaf chewers more than phloem feeders. However, if the change in fiber concentration also affected leaf quality for phloem feeders, for example, by changing phloem amino acid concentrations or by making the leaves tougher to penetrate, this could explain the relationship between phloem feeder density and cellulose concentration. Phloem feeder densities were low at the MID and HIGH elevation sites. Likewise, Marquis and Passoa (1989) found very few phloem feeders on striped maple trees at Mountain Lake Biological Station in western Virginia. It is unknown why *A. pensylvanicum* is not a preferred host plant of phloem feeders at mid and high elevations.

Similarly, *A. pensylvanicum* herbivore fauna in western Virginia consisted mostly of free living leaf-chewing generalist Lepidoptera, and herbivore densities were low throughout the season with peaks in July and August instead of the typical early season peak (Marquis and Passoa 1989). One possible factor behind the

low leaf chewer densities on striped maple during the early season is that other common tree species have higher quality leaves. Red oak (*Quercus rubra*) saplings are also locally abundant, and foliage collected from red oak saplings from the same locations contained 3.2–3.6% nitrogen 20 d after budburst compared with 2.4–2.6% for striped maple (C. B. Zehnder, unpublished data). Many of the Lepidoptera species that feed on *A. pensylvanicum* are highly polyphagous (Marquis and Passoa 1989) and may chose other tree species that have higher-quality leaves.

Leaf quality decreased throughout the growing season. Leaves were initially high in nitrogen and low in lignin (Fig. 2), and as the summer progressed, nitrogen concentrations decreased and lignin concentrations increased. Spatial and temporal variation in leaf quality has been observed in other temperate species including oak (Feeny 1970, Forkner and Hunter 2000), mountain birch (Haukioja et al. 1985, Ruusila et al. 2005), and tamarack (Powell and Raffa 1999). Rapidly developing striped maple foliage is a moving target, and these seasonal changes in leaf quality may prevent insect herbivores from adapting to and overcoming host plant defenses (Adler and Karban 1994, Ruusila et al. 2005).

Temporal variation in leaf quality was more substantial than was spatial variation. None of the foliar characteristics measured exhibited any consistent pattern with elevation, although there were differences among sites (Fig. 2). The lack of change along the elevational gradient is surprising. Phenolics provide photoprotective benefits to plants by acting as antioxidants and thereby protecting leaves from photo-induced oxidative damage (Close and McArthur 2002). Therefore, phenolic concentrations might be expected to increase with elevation because the risk of photodamage is higher at high elevations than at low elevations (Close and McArthur 2002). For example, UVB-absorbing compounds were found to increase with elevation in *Daphne laureola* (Alonso et al. 2005). In the study of Alonso et al. (2005), the elevational gradient ranged from 950 to 1,800 m. Our HIGH site was at 1,570 m; therefore, it is possible that increases in phenolic compound concentration only occur at higher elevations and that we would have documented a difference had we sampled a higher site. Although we found no evidence for an increase in total phenolics with elevation in this study, it is possible that individual compounds varied among the three sites and that our method of analysis prevented us from assessing this variation. Similarly, abiotic variation among the three sites did not influence lignin and cellulose concentrations, even though we predicted higher concentrations of these structural components at the more exposed high elevation site. However, we sampled from understory saplings, and these saplings were not exposed to as much abiotic stress as mature canopy trees. Increases in phenolic and fiber concentration with elevation may be more likely in mature canopy trees exposed to full sun and wind.

We conclude that, in this system, seasonal variation in plant quality is likely to be more important to insect

herbivores than is spatial variation in plant quality. Other factors such as the abiotic environment and natural enemies clearly play a role in addition to that of plant quality in determining herbivore distribution and abundance. As in some other systems (Preszler and Boecklen 1996), elevation is a consistent predictor of herbivore community structure on striped maple; leaf-chewing insects are always more abundant at high elevation, whereas exponential growth of aphid populations is facilitated at low elevation. However, we have little evidence to suggest that plant quality is the major driver of elevational patterns because spatial variation in foliar chemistry (Fig. 2) is not consistently associated with spatial variation in insect distribution or abundance (Fig. 1). We suggest that the abiotic environment and interactions with natural enemies may play a greater role in elevational patterns of herbivore community structure in striped maple than does plant quality.

Acknowledgments

We thank K. Leavelle, A. Mahoney, M. Parrish, L. Wilenbring, B. Ball, C. Hall, K. Wickings, W. Duncan, C. Frost, and M. Parris for field help. We thank T. Maddox and the Analytical Laboratory at the University of Georgia for foliar nitrogen analysis. The comments of three anonymous reviewers improved the quality of this manuscript. The research was supported by NSF Grant 0342750 to M.D.H. and R.J.C.

References Cited

- Abrahamson, W. G., M. D. Hunter, G. Melika, and P. W. Price. 2003. Cynipid gall-wasp communities correlate with oak chemistry. *J. Chem. Ecol.* 29: 208–223.
- Adler, F. R., and R. Karban. 1994. Defended fortresses or moving targets: another model of inducible defenses inspired by military metaphors. *Am. Nat.* 144: 813–832.
- Agrawal, A. A., N. Underwood, and J. R. Stinchcombe. 2004. Intraspecific variation in the strength of density-dependence in aphid populations. *Ecol. Entomol.* 29: 521–526.
- Allison, P. D. 1999. Logistic regression using SAS system: theory and application. SAS Institute, Cary, NC.
- Alonso, C., R. Perez, P. M. Nieto, and J. Delgado. 2005. Gender dimorphism and altitudinal variation of secondary compounds in leaves of the gynodioecious shrub *Daphne laureola*. *J. Chem. Ecol.* 31: 139–150.
- Barbosa, P., and A. Caldas. 2007. Seasonal patterns of parasitism and differential susceptibility among species in macrolepidopteran assemblages on *Salix nigra* (Marsh) and *Acer negundo* L. *Ecol. Entomol.* 32: 181–187.
- Bruelheide, H., and U. Scheidel. 1999. Slug herbivory as a limiting factor for the geographical range of *Arnica montana*. *J. Ecol.* 87: 839–848.
- Chen, M., and A. M. Shelton. 2007. Impact of soil type, moisture, and depth on swede midge (Diptera: Cecidomyiidae) pupation and emergence. *Environ. Entomol.* 36: 1349–1355.
- Cisneros, J. J., and L. D. Godfrey. 2001. Midseason pest status of the cotton aphid (Homoptera: Aphididae) in California cotton: is nitrogen a key factor? *Environ. Entomol.* 30: 501–510.
- Close, D. C., and C. McArthur. 2002. Rethinking the role of many plant phenolics: protection from photodamage not herbivores? *Oikos* 99: 166–172.
- Darrow, K., and M. D. Bowers. 1997. Phenological and population variation in iridoid glycosides of *Plantago lanceolata* (Plantaginaceae). *Biochem. Syst. Ecol.* 25: 1–11.
- Erelli, M. C., M. P. Ayres, and G. K. Eaton. 1998. Altitudinal patterns in host suitability for forest insects. *Oecologia (Berl.)* 117: 133–142.
- Feeny, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51: 565–572.
- Forkner, R. E., and M. D. Hunter. 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology* 81: 1588–1600.
- Forkner, R. E., R. J. Marquis, and J. T. Lill. 2004. Feeny revisited: condensed tannins as anti-herbivore defences in leaf-chewing herbivore communities of *Quercus*. *Ecol. Entomol.* 29: 174–187.
- Hall, M. C., P. Stiling, D. C. Moon, B. G. Drake, and M. D. Hunter. 2005. Effects of elevated CO₂ on foliar quality and herbivore damage in a scrub oak ecosystem. *J. Chem. Ecol.* 31: 267–286.
- Haukioja, E., P. Niemela, and S. Siren. 1985. Foliage phenols and nitrogen in relation to growth, insect damage, and ability to recover after defoliation, in the mountain birch *Betula pubescens* ssp. *tortuosa*. *Oecologia (Berl.)* 65: 214–222.
- Hengxiao, G., J. D. McMillin, M. R. Wagner, J. Zhou, Z. Zhou, and X. Xu. 1999. Altitudinal variation in foliar chemistry and anatomy of yunnan pine, *Pinus yunnanensis*, and pine sawfly (Hym., Diprionidae) performance. *J. Appl. Entomol.* 123: 465–471.
- Hibbs, D. E., B. F. Wilson, and B. C. Fischer. 1980. Habitat requirements and growth of striped maple (*Acer pensylvanicum*). *Ecology* 61: 490–496.
- Huberty, A. F., and R. F. Denno. 2006. Consequences of nitrogen and phosphorus limitation for the performance of two planthoppers with divergent life-history strategies. *Oecologia (Berl.)* 149: 444–455.
- Hunter, M. D. 1990. Differential susceptibility to variable plant phenology and its role in competition between two insect herbivores on oak. *Ecol. Entomol.* 15: 401–408.
- Kaplan, I., and R. F. Denno. 2007. Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecol. Lett.* 10: 977–994.
- Knoepp, J. D., and W. T. Swank. 1998. Rates of nitrogen mineralization across an elevation and vegetation gradient in the southern Appalachians. *Plant Soil.* 204: 235–241.
- Levesque, K. R., M. M. Fortina, and Y. Mauffette. 2002. Temperature and food quality effects on growth, consumption and post-ingestive utilization efficiencies of the forest tent caterpillar *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *Bull. Entomol. Res.* 92: 127–136.
- Littell, R. C., P. R. Henry, and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. *J. Anim. Sci.* 76: 1216–1231.
- Marquis, R. J., and S. Passoa. 1989. Seasonal diversity and abundance of the herbivore fauna of Striped Maple *Acer pensylvanicum* (Aceraceae) in Western Virginia. *Am. Midl. Nat.* 122: 313–320.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Annu. Rev. Ecol. Syst.* 11: 119–161.
- Powell, J. S., and K. F. Raffa. 1999. Sources of variation in concentration and composition of foliar monoterpenes in tamarack (*Larix laricina*) seedlings: roles of nutrient availability, time of season, and plant architecture. *J. Chem. Ecol.* 25: 1771–1797.
- Preszler, R. W., and W. J. Boecklen. 1996. The influence of elevation on tri-trophic interactions: opposing gradients

- of top-down and bottom-up effects on a leaf-mining moth. *Ecoscience* 3: 75–80.
- Reynolds, B. C., and D. A. Crossley. 1997. Spatial variation in herbivory by forest canopy arthropods along an elevation gradient. *Environ. Entomol.* 26: 1232–1239.
- Richardson, A. D. 2004. Foliar chemistry of balsam fir and red spruce in relation to elevation and the canopy light gradient in the mountains of the northeastern United States. *Plant Soil* 260: 291–299.
- Ritchie, M. E. 2000. Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. *Ecology* 81: 1601–1612.
- Rossiter, M. 1988. Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. *Ecology* 69: 267–277.
- Ruusila, V., J. P. Morin, T. van Ooik, I. Saloniemi, V. Ossipov, and E. Haukioja. 2005. A short-lived herbivore on a long-lived host: tree resistance to herbivory depends on leaf age. *Oikos* 108: 99–104.
- Salmore, A. K., and M. D. Hunter. 2001. Elevational trends in defense chemistry, vegetation, and reproduction in *Sanguinaria canadensis*. *J. Chem. Ecol.* 27: 1713–1727.
- Simonet, D. E., S. L. Clement, W. L. Rubink, and R. W. Rings. 1981. Temperature requirements for development and oviposition of *Peridroma saucia* (Lepidoptera: Noctuidae). *Can. Entomol.* 113: 891–897.
- Stiling, P., and D. C. Moon. 2005. Quality or quantity: the direct and indirect effects of host plants on herbivores and their natural enemies. *Oecologia* (Berl.) 142: 413–420.
- Strathdee, A. T., J. S. Bale, W. C. Block, S. J. Coulson, I. D. Hodkinson, and N. R. Webb. 1993. Effects of temperature elevation on a field population of *Acyrtosiphon svalbardicum* (Hemiptera: Aphididae) on Spitsbergen. *Oecologia* (Berl.) 96: 457–465.
- Suzuki, S. 1998. Leaf phenology, seasonal changes in leaf quality and herbivory pattern of *Sanguisorba tenuifolia* at different altitudes. *Oecologia* (Berl.) 117: 169–176.
- Swank, W. T., and D. A. Crossley. 1988. Introduction and site description, pp. 339–357. In W. T. Swank and D. A. Crossley (eds.), *Forest hydrology and ecology at Coweeta*. Springer, New York.
- Weston, P. A., and G. A. Desurmont. 2008. Pupation by viburnum leaf beetle (Coleoptera: Chrysomelidae): behavioral description and impact of environmental variables and entomopathogenic nematodes. *Environ. Entomol.* 37: 845–849.
- White, T.C.R. 1993. The inadequate environment: nitrogen and the abundance of animals. Springer, New York.
- Whittaker, N. P., and T. I. Tribe. 1998. Predicting numbers of an insect (*Neophilaenus lineatus*: Homoptera) in a changing climate. *J. Anim. Ecol.* 67: 987–991.
- Wikteliu, S. 1981. Diurnal flight periodicities and temperature thresholds for flight for different migrant forms of *Rhopalosiphum padi* L. (Hom., Aphididae). *Zeitschrift Angewandte Entomol.* 92: 449–457.
- Yarnes, C. T., and W. J. Boecklen. 2005. Abiotic factors promote plant heterogeneity and influence herbivore performance and mortality in Gambel's oak (*Quercus gambelii*). *Entomol. Exp. Appl.* 114: 87–95.

Received 18 December 2008; accepted 10 April 2009.