ÉCOSCIENCE

Increased per capita herbivory in the shade: Necessity, feedback, or luxury consumption?[1]

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Abstract: Leaf chemistry and physiology vary with light environment and are often thought to directly affect herbivory patterns. Biotic (*e.g.,* parasitoids and predators) and abiotic (*e.g.,* temperature, relative humidity) factors known to influence herbivory also co-vary with light environment. Irrespective of mechanism, light-based differences in herbivore damage must be the result of variable herbivore abundance, per capita effects, or both. We examined the effect of light environment on leaf defence and leaf nutritional quality in *Lindera benzoin* (Lauraceae) and relate this to the abundance and impact of its lepidopteran herbivore *Epimecis hortaria* (Lepidoptera: Geometridae). In this system we consistently observe greater natural field herbivory in shade habitats relative to high light habitats, despite similar herbivore abundances; differences in herbivory are therefore most likely attributable to different per capita impacts of herbivores across environments. Potential herbivore behaviours responsible for the observed field pattern include increased foraging per day and longer developmental periods in shade habitats. A more complete understanding of observed herbivory patterns requires incorporating variation in herbivore behaviour as influenced by abiotic or biotic factors that co-vary with the different light environments.
Keywords: *Epimecis hortaria*, leaf defences, leaf quality, light environment, *Lindera benzoin*, plant–herbivore interactions.

Résumé : La chimie et la physiologie de la feuille varient avec l'environnement lumineux et on considère généralement qu'ils influencent directement les patrons d'herbivorie. Les facteurs biotiques (par exemple les parasites et les prédateurs) et abiotiques (par exemple la température et l'humidité relative) influençant l'herbivorie covarient aussi avec l'environnement lumineux. Quel que soit le mécanisme en cause, les différences de dommages causés par l'herbivorie et attribuables à la lumière doivent être le résultat d'une variation de l'abondance des herbivores, des effets individuels ou des deux. Nous avons examiné l'effet de l'environnement lumineux sur les défenses de la feuille et ses qualités nutritionnelles chez *Lindera benzoin* (Lauraceae) et l'avons relié à l'abondance et l'impact de son herbivore lépidoptère *Epimecis hortaria* (Lepidoptera, Geometridae). Dans ce système en milieu naturel, nous observons toujours un taux d'herbivorie plus élevé dans les habitats ombragés que dans ceux très lumineux, malgré des abondances similaires d'herbivores; les différences de taux d'herbivorie sont donc très probablement attribuables à des différences d'impacts individuels entre ces environnements. Les comportements des herbivores potentiellement responsables des patrons observés en milieu naturel incluent une période journalière allongée au niveau de la quête alimentaire ou des périodes de développement plus longues dans les habitats ombragés. Une compréhension plus complète des patrons d'herbivorie observés nécessitera d'incorporer les variations du comportement des herbivores influencés par les facteurs abiotiques et biotiques qui covarient avec les différents environnements lumineux.
Mots-clés : défenses de la feuille, environnement lumineux, *Epimecis hortaria*, interactions plante-herbivore, *Lindera benzoin*, qualité de la feuille.

Nomenclature: Gleason & Cronquist, 1991.

Introduction

The effect of light environment on herbivory has been the focus of much study (Bryant, Chapin & Klein, 1983; Coley, 1983; Louda & Rodman, 1983; Coley, Bryant & Chapin, 1985; Larsson *et al.,* 1986; Coley, 1988; Aide & Zimmerman, 1990; Lindroth *et al.,* 1993; Dudt & Shure, 1994; Sagers & Coley, 1995; Crone & Jones, 1999). This makes sense given that plants, particularly those in the forest understory, can occur in a wide range of light conditions and are often light-limited. Additionally, plant growth rates, which are typically strongly related to light levels, can also indirectly affect, or be affected, by allocation to defence (Bryant, Chapin & Klein, 1983; Coley, Bryant & Chapin, 1985; Herms & Mattson, 1992; Zangerl, Arntz & Berenbaum, 1997; Stamp, 2003).

Light environment can affect the nutritional quality of leaves by causing variation in the amount and chemical form of nitrogen, carbon, and other elements experienced by consumers (Scriber & Slansky, 1981; Bryant, Chapin & Klein, 1983). For instance, plants in low light environments are often carbon limited and have been observed to have fewer carbohydrates (Koricheva *et al.,* 1998; Henriksson *et al.,* 2003), fewer total phenolics (Dudt & Shure, 1994; Koricheva *et al.,* 1998), greater relative and

absolute amounts of nitrogen (Aide & Zimmerman, 1990; Henriksson *et al.*, 2003; but equivocal in Koricheva *et al.*, 1998), as well as higher water content (Aide & Zimmerman, 1990; Henriksson *et al.*, 2003). Variation in light environment can also influence structural defences, including decreased leaf toughness in low light environments (Aide & Zimmerman, 1990; Dudt & Shure, 1994; Henriksson *et al.*, 2003). The specific manner in which plant nutritional quality, defensive characteristics, and their interaction account for variation in herbivory rates among sun and shade populations of plants is an open question.

Although leaves from plants in shade environments are theoretically predicted to be better food sources for herbivores (Bryant, Chapin & Klein, 1983; Herms & Mattson, 1992; but see Stamp, 2003), evidence for a general pattern of increased levels of herbivory in shade environments is equivocal (Koricheva *et al.*, 1998; Stamp, 2003). Previous studies have observed increased herbivory in shade environments (Lincoln & Langenheim, 1979; Niesenbaum, 1992b; Shure & Wilson, 1993; Valladares, Salvo & Cagnolo, 2006), herbivore preference for shade-grown leaves (Folgarait *et al.*, 1996; Crone & Jones, 1999), or increased herbivore performance on leaves from shade-grown plants (Lindroth *et al.*, 1993; Henriksson *et al.*, 2003). Other studies examining the relationship between light environment and herbivory have observed greater herbivory in high light environments (Lincoln & Mooney, 1984; Louda & Rodman, 1996; McGeoch & Gaston, 2000; Chacon & Armesto, 2006), preference for leaves from sun plants (Nichols-Orians, 1991), and improved herbivore performance on sun-plant leaves (Fortin & Mauffette, 2001; Levesque, Fortin & Mauffette, 2002; Niesenbaum & Kluger, 2006).

The aim of this study was to investigate the impact of light environment on leaf defence and nutritional quality in *Lindera benzoin* (northern spicebush; Lauraceae) in relationship to the consistent patterns of abundance and leaf damage inflicted by its primary herbivore, *Epimecis hortaria* (tulip tree beauty; Lepidoptera: Geometridae). Specifically, we asked 1) how light environment influences *Lindera benzoin* leaf chemistry and defence and 2) how this relates to patterns of herbivore abundance and damage. We discuss our results in light of other studies from our particular system and the broader field of light-environment effects on herbivore–host plant interactions.

Methods

STUDY SITE

Research was conducted at 2 sites in eastern Pennsylvania: the Lee and Virginia Graver Arboretum in Northampton County (hereafter Graver) and the Conrad W. Raker Biological Field Station and Wildlife Sanctuary in Lehigh County (hereafter Raker). Both sites support large numbers of *L. benzoin* in both sun and shade environments. Typical of the mesophytic deciduous forests of this region (Braun, 1950), the overstories of our study sites are dominated by *Acer rubrum* (Aceraceae), *Fagus grandifolia* (Fagaceae), *Liriodendron tulipifera* (Magnoliaceae), *Juglans nigra* (Juglandaceae), and various *Quercus* (Fagaceae) and *Carya* (Juglandaceae) species. The understory shrub layer

is a near monoculture of *L. benzoin*. Sun-designated habitats (forest edges and large tree-fall gaps) had an absent or quite thin overstory, while shade habitats were under relatively intact overstory. The mean (SE) incident photosynthetically active radiation (PAR) (μmol·m^{-2}·s^{-1}) at mid-day was 658.30 ($\pm$ 77.63) in designated sun habitats and 48.01 ($\pm$ 8.61) in the shade. While we cannot account for the role of other environmental factors that likely covaried with light environment (*e.g.,* temperature, relative humidity, edge-effects, etc.), it is difficult to minimize the potential impact of light given the generally light-limited nature of northeastern temperate forests (Botkin, Wallis & Janak, 1972).

STUDY SPECIES

Lindera benzoin (Lauraceae), or northern spicebush, is a common understory shrub in moist forests of eastern North America from southern Ontario to Florida. The plant is considered shade-adapted but occurs in a range of light conditions from deep shade within the forest understory to bright light on forest edge and in tree-fall gaps. *Lindera benzoin* flowers in early April, and leaves emerge and new vegetative growth begins in mid-May (Niesenbaum, 1992b). Herbivory by lepidopteran larvae becomes apparent on the leaves by late June and is easily distinguished and measured (Niesenbaum, 1992a).

The primary herbivore in this system is the larva of *Epimecis hortaria* (Lepidoptera: Geometridae). *Epimecis hortaria* is oligophagous and has been observed in other habitats feeding on a limited number of species, including *L. benzoin, Sassafras albidum* (sassafras; Lauraceae), and *Liriodendron tulipifera* (tulip poplar; Magnoliaceae). At our study sites *E. hortaria* feeding is largely restricted to *L. benzoin* due to the infrequency of other hosts. We observe very little damage to *L. benzoin* by other insects. In this system we have continuously observed patterns of greater herbivore damage to *L. benzoin* in shade habitats relative to high light environments, despite similar abundances of *E. hortaria* (Niesenbaum, 1992b; Niesenbaum & Kluger, 2006), including in the year of this study.

HERBIVORE DAMAGE AND ABUNDANCE

In August 2005 we estimated the amount of spicebush leaf herbivory by randomly sampling 20 leaves at each of 4 sun and 4 shade plots at both field sites. Leaf area consumed was measured per leaf using the Win-DIAS image analysis system (Delta-T Devices Ltd., Cambridge, UK). Data were log transformed and analyzed by ANOVA using JMP (version 5.1, SAS institute, Cary, North Carolina, USA) with field site (Raker *versus* Graver, fixed effect) and habitat type (sun *versus* shade, fixed effect) as main effects and plot (nested within site and habitat type, random effect) as a nested effect. Data were checked for deviations from normality and heteroscedasticity. No transformations were necessary.

Epimecis hortaria abundance was measured in sun and shade plots at both field sites. Approximately 1 m of stem material per shrub was systematically shaken over a beat sheet and the number of larvae was recorded. Sites were sampled twice weekly over the course of the growing season (8 times total). Abundance data were analyzed by ANOVA as

above. Data were checked for deviations from normality and heteroscedasticity. No transformations were necessary.

SPICEBUSH LEAF CHARACTERISTICS

Two to three mature leaves (defined as the leaves growing at the base of branches) were collected at both sites from 5 separate branches from each of 10 plants per habitat type. Immediately upon returning to the laboratory, fresh mass of leaves was recorded and leaf toughness was determined by the force required to puncture the leaf surface with a digital force gauge penetrometer (MG05, Mark-10, Copiague, New York, USA). Following toughness measurement, samples were dried at 60 °C to constant mass, reweighed, and ground by Wiley Mill (60 mesh). Percent leaf C and N were determined using an EA1112 Flash CHN automatic elemental analyzer (Thermo Electron Corporation, Waltham, Massachusetts, USA).

Sample extracts to determine soluble protein and non-structural carbohydrate contents were prepared after the method of Bauer, Berntson, and Bazzaz (2001). Analysis of protein content was based on the method of Bradford (1976), using Bovine Serum Albumin as the standard and absorbance determined by a microplate spectrophotometer (μQuant, Bio-Tek instruments, Winooski, Vermont, USA). Nonstructural carbohydrate content was determined colorimetrically by the anthrone–sulfuric acid method (Dreywood, 1946), reading absorbance at 600 nm by UV/Vis spectrophotometer (Perkin Elmer, Shelton, Connecticut, USA).

Spicebush branch data were pooled and the resulting plant averages were analyzed as a two-way ANOVA, with site (Graver *versus* Raker, fixed effect) and habitat type (sun *versus* shade, fixed effect) as main effects. All data were checked for deviations from normality and heteroscedasticity. No transformations were necessary.

Total phenolics and tannins were determined from mature leaves harvested from 10 individuals each from sun and shade habitats at the Graver site. Leaf samples were ground with mortar and pestle in liquid nitrogen. Extracts were prepared using 70% aqueous acetone. Total phenolics were measured as tannic acid equivalents using the Folin–Ciocalteu method (Folin & Ciocalteu, 1927; Waterman & Mole, 1994). Absorbance was measured at 760 nm by UV/Vis spectrophotometer. Following total phenolic measurement, polyvinylpyrrolidone (PVP) was added to the plant extract to bind tannins. Tannin content was determined by subtracting this latter non-tannin phenolic content from the former total phenolic content (Andersen & Sowers, 1968). Total phenolic and tannin content were analyzed using a one-way ANOVA to identify the influence of habitat (sun or shade, fixed effect). Data were checked for deviations from normality and heteroscedasticity. Accordingly, both total phenolic and tannin contents were log transformed (Sokal & Rohlf, 1995).

Results

HERBIVORE DAMAGE AND ABUNDANCE

Average leaf area consumed by herbivores varied significantly by habitat type ($F_{1, 12} = 8.56$, $P = 0.0037$). Levels of herbivory were 50% greater in shade plots compared to sun plots (Least squares mean $[LSM]_{sun} = 2.0$ cm^2, $LSM_{shade} = 3.0$ cm^2, Figure 1a).

The number of *E. hortaria* larvae feeding on *L. benzoin* did not significantly vary by habitat type ($F_{1, 36} = 1.07$, $P = 0.3068$). Mean abundances of *E. hortaria* per sampling period were 0.9 larvae in sun habitats and 1.3 larvae in shade areas (Figure 1b). *Epimecis hortaria* abundance far outnumbered all other herbivorous insects at our sites.

SPICEBUSH LEAF CHARACTERISTICS

There was a significant effect of habitat type and plant on percent leaf water content (Table I). Leaves from shade plants had 5% greater mass composed of water compared to leaves from sun plants ($LSM_{sun} = 67\%$, $LSM_{shade} = 73\%$). There was also a small, but statistically significant difference between sites ($LSM_{Graver} = 71\%$, $LSM_{Raker} = 69\%$).

Leaves from *L. benzoin* growing in sunlit environments had significantly greater C/N ratios compared to those from plants growing in shaded areas (Table I, $LSM_{sun} = 22.9$, $LSM_{shade} = 20.1$, Figure 2a). There was also a significant effect of site on leaf C/N ratio (Table I, $LSM_{Graver} = 19.8$, $LSM_{Raker} = 23.2$). The differences in C/N ratio reflect the
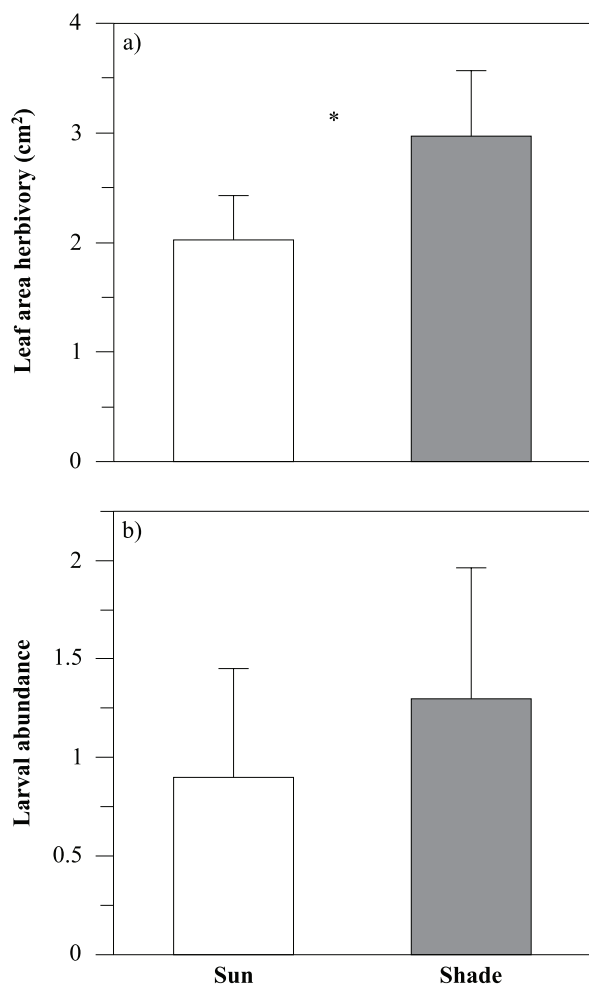

FIGURE 1. Least squares means for a) leaf herbivory and b) larval abundance per metre of branch material in sun (open bars) and shade (filled bars) plots. Error bars represent 95% confidence intervals. Asterisks indicate statistically significant differences ($P < 0.05$).

TABLE I. ANOVAs assessing the effect of site (Graver *versus* Raker) and habitat type (sun *versus* shade) on leaf traits (% water content, C/N ratio, soluble proteins, nonstructural carbohydrates, and toughness). For each factor we report the numerator degrees of freedom (df num), denominator degrees of freedom (df den), *F*, and *P*-values. Statistically significant effects at the *P* < 0.05 value are highlighted in boldface.

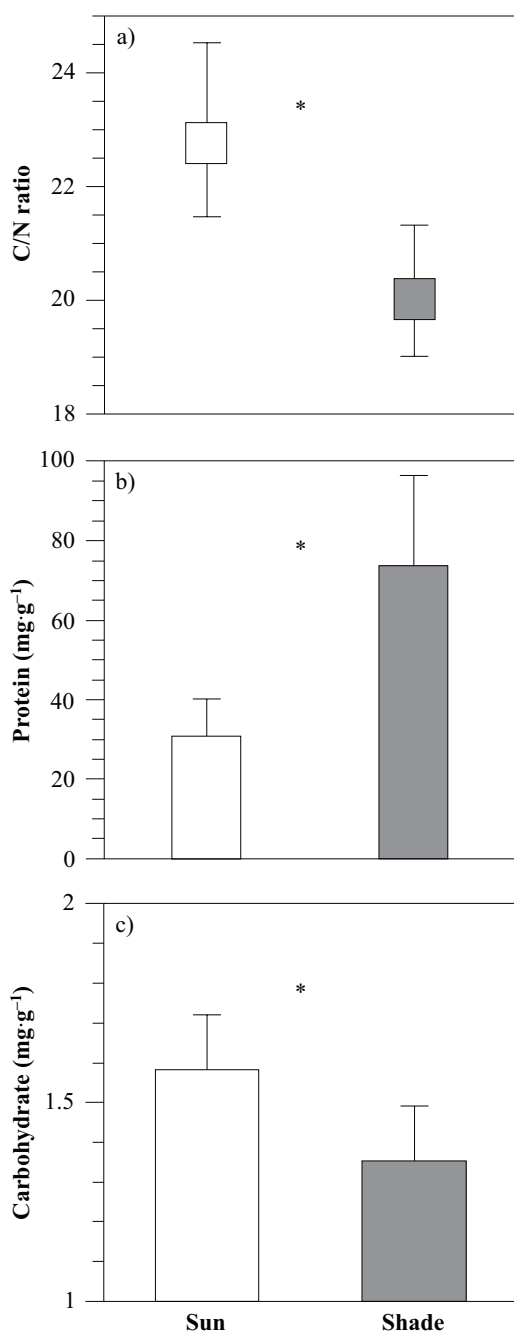| Source	df num, df den	% water		C/N ratio		Protein		Carbohydrates		Toughness	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Site (S)	1, 36	**4.47**	**0.041**	**11.96**	**0.001**	0.16	0.692	**7.51**	**0.010**	2.9	0.097
Habitat (H)	1, 36	**34.14**	**< 0.001**	**8.09**	**0.007**	**18.34**	**0.001**	**5.42**	**0.026**	**31.95**	**< 0.001**
S × H	1, 36	0.09	0.764	0.057	0.813	2.42	0.129	2.7	0.109	2.87	0.099

FIGURE 2. Least squares means for leaf a) C/N ratio, b) soluble protein (mg·g^{-1} leaf tissue), and c) nonstructural carbohydrate content (mg·g^{-1} leaf tissue) in sun (open symbols and bars) and shade (filled symbols and bars) plots. Error bars represent 95% confidence intervals. Asterisks indicate statistically significant differences (*P* < 0.05).

combined result of both greater percent C ($F_{1, 36}$ = 26.50, *P* > 0.0001, LSM $_{sun}$ = 48.1, LSM $_{shade}$ = 46.8) and lower percent N ($F_{1, 36}$ = 5.56, *P* = 0.0239, LSM $_{sun}$ = 2.2, LSM $_{shade}$ = 2.4) in sun habitats. There was also a statistically significant site by habitat interaction for percent C ($F_{1, 36}$ = 9.52, *P* = 0.0039); the nature of the difference between sun and shade plants was similar across sites, but of a greater magnitude at Raker.

Consistent with the greater C/N ratio in sunlit habitats, leaves from *L. benzoin* growing in this habitat had significantly less protein content compared to leaves from plants growing in shade habitats (Table I, LSM $_{sun}$ = 30.9 mg·g^{-1}, LSM $_{shade}$ = 73.8 mg·g^{-1}, Figure 2b). Also consistent with the C/N ratio pattern, leaves from sun plants had significantly greater nonstructural carbohydrate content compared to leaves from shade plants (Table I, LSM $_{sun}$ = 1.58 mg·g^{-1}, LSM $_{shade}$ = 1.35 mg·g^{-1}, Figure 2c). There was also a significant effect of site on leaf carbohydrate content (Table I, LSM $_{Graver}$ = 1.33 mg·g^{-1}, LSM $_{Raker}$ = 1.60 mg·g^{-1}).

Habitat type was the only main effect that significantly influenced leaf toughness in *L. benzoin* leaves (Table I). The average force required to puncture leaves from sun plants was approximately 31% greater than that necessary to puncture leaves from shade plants (LSM $_{sun}$ = 61.7 g, LSM $_{shade}$ = 47.3 g, Figure 3a).

There were no statistically significant effects of habitat type on either leaf total phenolics (LSM = 16.1 mg·g^{-1}, $F_{1, 14}$ = 0.0047, *P* = 0.9463, Figure 3b) or tannin content (LSM = 5.9 mg·g^{-1}, $F_{1, 14}$ = 0.1029, *P* = 0.7531, Figure 3c).

Discussion

There are multiple hypotheses that may explain why *per capita* herbivory varies with leaf quality. (1) Individual herbivores may be expected to inflict greater *per capita* damage on lower food quality leaves out of necessity (to maintain fitness). A "necessity consumption" explanation might be particularly likely if fitness varies discontinuously with larval size or developmental stage, increasing predominantly at certain thresholds. For example, there may exist a minimum mass necessary to allow successful pupation or emergence (that, in turn, could result in hard selective pressures). (2) Individual herbivores on high-quality leaves might inflict greater *per capita* damage because of positive feedback between leaf quality and herbivore ability. In this "feedback consumption" hypothesis, higher food quality leaves may cause larvae to grow faster, and faster growing larvae may be able to eat greater amounts of leaf tissue. (3) In favourable environments, individual herbivores may

consume leaf tissue beyond their basic needs in order to gain a fitness advantage at future life stages. This "luxury consumption" might be expected to occur when the relationship between fitness and biomass is predominantly linear, in which case each additional mass of tissue consumed may contribute to future fitness (Chapin, 1980; Nicholls,
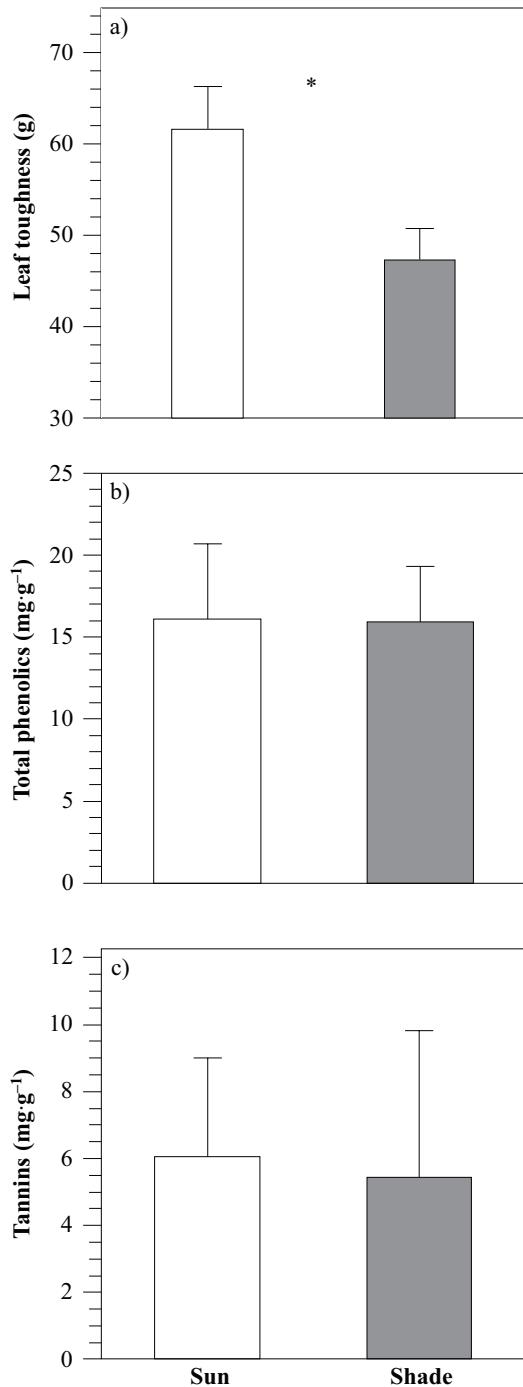

FIGURE 3. Least squares means for leaf a) toughness (g), b) total phenolic content (mg·g^{-1} leaf tissue), and c) tannin content (mg·g^{-1} leaf tissue) in sun (open bars) and shade (filled bars) plots. Error bars represent 95% confidence intervals. Asterisks indicate statistically significant differences ($P < 0.05$). Means presented are back transformed or non transformed values (see Methods for details).

1987; Lynn *et al.,* 2000; Sterner & Schwalbach, 2001). For example, larger larvae may have greater successful pupation or emergence rates (that, in turn, could result in soft selection pressures). It is important to note that these hypotheses are not mutually exclusive: while individual larvae on low-quality plants may need to consume more leaf tissue to successfully pass certain developmental hurdles (*e.g.,* successful progression to adult stage, "necessity foraging"), larvae on nearby high-quality plants may exhibit increased rates of leaf consumption due to their greater vigour ("feedback foraging") and may continue to feed beyond current needs to increase fitness at some point in the future (*e.g.,* greater egg production or mating bouts as adult, "luxury foraging").

Leaf-level variability that potentially contributed to differences in the *per capita* effect of herbivores can broadly be grouped into leaf defence and leaf quality. With respect to defence, all else being equal, leaves that are less well defended would be expected to suffer greater rates of damage from herbivores. In partial confirmation of this prediction we found that tougher leaves from *L. benzoin* growing in high light environments experienced significantly less herbivory. However, we found no difference in the amount of total phenolics or tannins between leaves from sun and shade plants. It is possible that other defensive compounds not examined here (*e.g.,* terpenes, alkaloids) may be more variable with light environment.

With respect to variation in leaf quality, we found that leaves from shade-grown plants had a significantly greater relative amount of nitrogen, significantly greater absolute amounts of soluble proteins, and fewer nonstructural carbohydrates than leaves from sun-grown *L. benzoin* (although differences in carbohydrates were very small compared to the former). While it is predicted that nitrogen content will be greater in high light habitats, where photosynthesis activity is greater, others have also reported the opposite pattern (Hemming & Lindroth, 1999; Osier & Lindroth, 2006). If nitrogen content is a primary determinant of herbivore growth (Scriber & Slansky, 1981; Ritchie, 2000), our findings suggest that *L. benzoin* leaves from shade habitats should be more nutritious for *E. hortaria*. However, Niesenbaum and Kluger (2006) found that efficiencies of conversion of leaf area and leaf mass to larval biomass of third instar *E. hortaria* were actually significantly greater when reared on leaves from sun-grown plants. There were, however, no differences in larval mass gain per leaf dry mass consumed (R. A. Niesenbaum, unpubl. data), suggesting that efficiencies of conversion of larva feeding on shade leaves may be compromised by the large amounts of water that dilute the otherwise similar food quality of these leaves.

Relatively few previous studies have linked studies of the effects of light environment on herbivore abundance and impact in the same system. In the spicebush system, as we consistently observe no difference in abundance of the primary herbivore across light environments, differences in herbivore impact are most likely the result of different *per capita* effects of herbivores. We rule out differences in total phenolic content as an explanation for *per capita* feeding differences, and previous work suggests we can exclude the direct effect of temperature on feeding rate, though not necessarily its effect on total developmental time or possible indirect effects (Niesenbaum & Kluger, 2006). It is possible

that greater leaf toughness in sun habitats contributes to the observed pattern, although lab and field trials suggest that leaf toughness does not actually reduce the amount of herbivory in the short term. The possibility of feedback foraging can also be ruled out, as increased growth rates of herbivores did not result in greater damage to leaves. Instead, it seems likely that the increase in *per capita* herbivory in the shade is either the result of luxury consumption of N-rich shade leaves or necessity consumption of the more diluted shade leaves. In either case it remains unknown whether increased herbivory in the shade is the result of prolonged larval periods, more time spent foraging per day, or both.

While light availability is known to be a primary factor influencing phenotypic variability, species interactions, and trophic dynamics, it is also well known that variation in light environment is correlated with a host of other abiotic and biotic factors, making the detection and description of causal relationships in any given study a difficult task (Dunson & Travis, 1991; Larsson, Haggstrom & Denno, 1997; Ritchie, 2000; Ewers & Didham, 2006). In our study system, variation in light environment contributes to altered leaf chemistry (greater percent N and soluble proteins in the shade, greater percent C and nonstructural carbohydrates in the sun), leaf physiology (greater percent water in the shade), leaf defence (greater leaf toughness in the sun), and herbivore activity (greater *per capita* herbivory in the shade). Furthermore, the effects of particular leaf traits on rates of herbivory appear to be more important than others (*e.g.,* N availability and water content). A more complete understanding of the observed increased *per capita* herbivory in shade environments would include the potential effects of light environment on other relevant abiotic (*e.g.,* relative humidity, Dunson & Travis, 1991; Larsson, Haggstrom & Denno, 1997) and biotic variables (*e.g.,* predator and parasitoid activity, McGeoch & Gaston, 2000; Sipura & Tahvanainen, 2000; Schmitz, 2005; Valladares, Salvo & Cagnolo, 2006) that are likely to influence herbivore activity.

Acknowledgements

Literature cited

Aide, T. M. & J. K. Zimmerman, 1990. Patterns of insect herbivory, growth, and survivorship in juveniles of a neotropical liana. Ecology, 71: 1412–1421.

Andersen, R. A. & J. A. Sowers, 1968. Optimum conditions for bonding of plant phenols to insoluble polyvinylpyrrolidone. Phytochemistry, 7: 293–301.

Bauer, G. A., G. M. Berntson & F. A. Bazzaz, 2001. Regenerating temperate forests under elevated CO_2 and nitrogen deposition: Comparing biochemical and stomatal limitation of photosynthesis. New Phytologist, 152: 249–266.

Botkin, D. B., J. R. Wallis & J. F. Janak, 1972. Some ecological consequences of a computer model of forest growth. Journal of Ecology, 60: 849–872.

Bradford, M. M., 1976. Rapid and sensitive method for quantitation of microgram quantities of protein utilizing principle of protein-dye binding. Analytical Biochemistry, 72: 248–254.

Braun, E. L., 1950. Deciduous Forests of Eastern North America. Free Press, New York, New York.

Bryant, J. P., F. S. Chapin & D. R. Klein, 1983. Carbon nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos, 40: 357–368.

Chacon, P. & J. J. Armesto, 2006. Do carbon-based defences reduce foliar damage? Habitat-related effects on tree seedling performance in a temperate rainforest of Chiloe Island, Chile. Oecologia, 146: 555–565.

Chapin, F. S., 1980. The mineral-nutrition of wild plants. Annual Review of Ecology and Systematics, 11: 233–260.

Coley, P. D., 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecological Monographs, 53: 209–233.

Coley, P. D., 1988. Effects of plant-growth rate and leaf lifetime on the amount and type of anti-herbivore defense. Oecologia, 74: 531–536.

Coley, P. D., J. P. Bryant & F. S. Chapin, 1985. Resource availability and plant antiherbivore defense. Science, 230: 895–899.

Crone, E. E. & C. G. Jones, 1999. The dynamics of carbon–nutrient balance: Effects of cottonwood acclimation to short- and long-term shade on beetle feeding preferences. Journal of Chemical Ecology, 25: 635–656.

Dreywood, R., 1946. Qualitative test for carbohydrate material. Industrial and Engineering Chemistry-Analytical Edition, 18: 499.

Dudt, J. F. & D. J. Shure, 1994. The influence of light and nutrients on foliar phenolics and insect herbivory. Ecology, 75: 86–98.

Dunson, W. A. & J. Travis, 1991. The role of abiotic factors in community organization. American Naturalist, 138: 1067–1091.

Ewers, R. M. & R. K. Didham, 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews, 81: 117–142.

Folgarait, P. J., L. A. Dyer, R. J. Marquis & H. E. Braker, 1996. Leaf-cutting ant preferences for five native tropical plantation tree species growing under different light conditions. Entomologia Experimentalis et Applicata, 80: 521–530.

Folin, O. & V. Ciocalteu, 1927. On tyrosine and tryptophane determinations in proteins. Journal of Biological Chemistry, 73: 627–650.

Fortin, M. & Y. Mauffette, 2001. Forest edge effects on the biological performance of the forest tent caterpillar (Lepidoptera: Lasiocampidae) in sugar maple stands. Écoscience, 8: 164–172.

Gleason, H. A. & A. Cronquist, 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. New York Botanical Garden Press, Bronx, New York.

Hemming, J. D. C. & R. L. Lindroth, 1999. Effects of light and nutrient availability on aspen: Growth, phytochemistry, and insect performance. Journal of Chemical Ecology, 25: 1687–1714.

Henriksson, J., E. Haukioja, V. Ossipov, S. Ossipova, S. Sillanpaa, L. Kapari & K. Pihlaja, 2003. Effects of host shading on consumption and growth of the geometrid *Epirrita autumnata*: Interactive roles of water, primary and secondary compounds. Oikos, 103: 3–16.

Herms, D. A. & W. J. Mattson, 1992. The dilemma of plants: To grow or defend. Quarterly Review of Biology, 67: 283–335.

Koricheva, J., S. Larsson, E. Haukioja & M. Keinanen, 1998. Regulation of woody plant secondary metabolism by resource availability: Hypothesis testing by means of meta-analysis. Oikos, 83: 212–226.

Larsson, S., H. E. Haggstrom & R. F. Denno, 1997. Preference for protected feeding sites by larvae of the willow-feeding leaf beetle *Galerucella lineola*. Ecological Entomology, 22: 445–452.

Larsson, S., A. Wiren, L. Lundgren & T. Ericsson, 1986. Effects of light and nutrient stress on leaf phenolic chemistry in *Salix dasyclados* and susceptibility to *Galerucella lineola* (Coleoptera). Oikos, 47: 205–210.

Levesque, K. R., M. Fortin & 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). Bulletin of Entomological Research, 92: 127–136.

Lincoln, D. E. & J. H. Langenheim, 1979. Variation of *Satureja douglasii* monoterpenoids in relation to light-intensity and herbivory. Biochemical Systematics and Ecology, 7: 289–298.

Lincoln, D. E. & H. A. Mooney, 1984. Herbivory on *Diplacus aurantiacus* shrubs in sun and shade. Oecologia, 64: 173–176.

Lindroth, R. L., P. B. Reich, M. G. Tjoelker, J. C. Volin & J. Oleksyn, 1993. Light environment alters response to ozone stress in seedlings of *Acer saccharum* Marsh. and hybrid *Populus* L. III. Consequences for performance of gypsy moth. New Phytologist, 124: 647–651.

Louda, S. M. & J. E. Rodman, 1983. Concentration of glucosinolates in relation to habitat and insect herbivory for the native crucifer *Cardamine cordifolia*. Biochemical Systematics and Ecology, 11: 199–207.

Louda, S. M. & J. E. Rodman, 1996. Insect herbivory as a major factor in the shade distribution of a native crucifer (*Cardamine cordifolia* A. Gray, bittercress). Journal of Ecology, 84: 229–237.

Lynn, S. G., S. S. Kilham, D. A. Kreeger & S. J. Interlandi, 2000. Effect of nutrient availability on the biochemical and elemental stoichiometry in the freshwater diatom *Stephanodiscus minutulus* (Bacillariophyceae). Journal of Phycology, 36: 510–522.

McGeoch, M. A. & K. J. Gaston, 2000. Edge effects on the prevalence and mortality factors of *Phytomyza ilicis* (Diptera, Agromyzidae) in a suburban woodland. Ecology Letters, 3: 23–29.

Nicholls, K. H., 1987. Predation on *Synura* spp. (Chrysophyceae) by *Bodo crassus* (Bodonaceae). Transactions of the American Microscopical Society, 106: 359–363.

Nichols-Orians, C. M., 1991. The effects of light on foliar chemistry, growth and susceptibility of seedlings of a canopy tree to an attine ant. Oecologia, 86: 552–560.

Niesenbaum, R. A., 1992a. Sex-ratio, components of reproduction, and pollen deposition in *Lindera benzoin* (Lauraceae). American Journal of Botany, 79: 495–500.

Niesenbaum, R. A., 1992b. The effects of light environment on herbivory and growth in the dioecious shrub *Lindera benzoin* (Lauraceae). American Midland Naturalist, 128: 270–275.

Niesenbaum, R. A. & E. C. Kluger, 2006. When studying the effects of light on herbivory, should one consider temperature? The case of *Epimecis hortaria* F. (Lepidoptera: Geometridae) feeding on *Lindera benzoin* L. (Lauraceae). Environmental Entomology, 35: 600–606.

Osier, T. L. & R. L. Lindroth, 2006. Genotype and environment determine allocation to and costs of resistance in quaking aspen. Oecologia, 148: 293–303.

Ritchie, M. E., 2000. Nitrogen limitation and trophic *versus* abiotic influences on insect herbivores in a temperate grassland. Ecology, 81: 1601–1612.

Sagers, C. L. & P. D. Coley, 1995. Benefits and costs of defense in a neotropical shrub. Ecology, 76: 1835–1843.

Schmitz, O. J., 2005. Scaling from plot experiments to landscapes: Studying grasshoppers to inform forest ecosystem management. Oecologia, 145: 225–234.

Scriber, J. M. & F. Slansky, 1981. The nutritional ecology of immature insects. Annual Review of Entomology, 26: 183–211.

Shure, D. J. & L. A. Wilson, 1993. Patch-size effects on plant phenolics in successional openings of the southern Appalachians. Ecology, 74: 55–67.

Sipura, M. & J. Tahvanainen, 2000. Shading enhances the quality of willow leaves to leaf beetles—but does it matter? Oikos, 91: 550–558.

Sokal, R. R. & F. J. Rohlf, 1995. Biometry. W.H. Freeman & Company, New York, New York.

Stamp, N., 2003. Out of the quagmire of plant defense hypotheses. Quarterly Review of Biology, 78: 23–55.

Sterner, R. W. & M. S. Schwalbach, 2001. Diel integration of food quality by *Daphnia*: Luxury consumption by a freshwater planktonic herbivore. Limnology and Oceanography, 46: 410–416.

Valladares, G., A. Salvo & L. Cagnolo, 2006. Habitat fragmentation effects on trophic processes of insect–plant food webs. Conservation Biology, 20: 212–217.

Waterman, P. G. & S. Mole, 1994. Analysis of plant phenolic metabolites. Blackwell Scientific Publications, Boston, Massachusetts.

Zangerl, A. R., A. M. Arntz & M. R. Berenbaum, 1997. Physiological price of an induced chemical defense: Photosynthesis, respiration, biosynthesis, and growth. Oecologia, 109: 433–441.