Combined Effects of Host Plant Quality and Predation on a Tropical Lepidopteran: A Comparison between Treefall Gaps and the Understory in Panama

Lora A. Richards[1,3] and **Phyllis D. Coley**[1,2]

[1]Department of Biology, University of Utah, 257 S. 1400 E., Salt Lake City Utah 84112, U.S.A.

[2]Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancon, Rep. of Panama

ABSTRACT

In tropical forests, light-gaps created from treefalls are a frequent source of habitat heterogeneity. The increase in productivity, through gap formation, can alter food quality, predation and their impact on insect herbivores. We hypothesized that in gaps, herbivores would be less resource-limited and more predator limited, whereas in the understory, we predicted the reverse. In this study, we investigate the combined effects of food quality and predation on the lepidopteran larva *Zunacetha annulata* feeding on its host plant *Hybanthus prunifolius* in two habitats; sunny treefall gaps and the shaded understory in Panama. In bioassays, *Z. annulata* feeding on sun leaves ate 22 percent less leaf area, grew 25 percent faster, and had higher pupal weights than larvae feeding on shade leaves. However, shade leaves had higher nitrogen content and specific leaf area. In gaps, predation was 26.4 percent compared to 13.8 percent in the understory. Larvae on understory plants traveled greater distances and spent more time searching and traveling than larvae on gap plants. These differences in behavior are consistent with lower predation risk and lower quality food in the understory. Using data from bioassays and field experiments we calculated 0.22 percent and 1.02 percent survival to adulthood for larvae in gaps and the understory, respectively. In conclusion, although these habitats were in close proximity, we found that larvae in the understory are more resource-limited and larvae in gaps are more predator limited.

Key words: bioassays; herbivory rates; *Hybathus prunifolius*; Pamana; predation rates; *Zunacetha annulata*.

HERBIVOROUS INSECTS ARE INFLUENCED BY A COMBINATION of the quality of food resources, natural enemy abundance, and abiotic conditions (Kingsolver 1989; Stamp & Bowers 1990, 1994; Chase 1996; Ritchie 2000). In addition, the relative impact of food availability and natural enemies on herbivores can vary with productivity (Oksanen *et al.* 1981, Fretwell 1987, Abrams 1993, Fraser & Grime 1997). In natural ecosystems, these influences are spatially variable and heterogeneous (Hunter & Price 1992, Persson 1999, Abrams 2000).

Light availability is a common source of variability in food resources, natural enemies, and abiotic conditions. Thus, in neighboring sunny and shady habitats herbivores will be subject to different pressures (Maiorana 1981). An increase in light availability can increase local productivity with increased plant growth, which in turn can affect populations of both herbivores and natural enemies. For example, when tropical canopy trees fall, a habitat of high light is created on the otherwise light-limited forest floor. In response to the formation of these high light environments, plant productivity increases through an increase in seedling establishment, survival, and growth (summarized by Denslow 1987). This increase in productivity has implications for the interactions between plants, herbivores, and natural enemies (Richards & Coley 2007). It is predicted that predators would have a greater impact on prey (herbivores) in patches of high productivity compared to lower productivity (Hochberg & van Baalen 1998). Previous studies in Panama (Harrison 1987, Richards & Coley 2007) found that herbivores in gaps were exposed to higher predation rates than herbivores in the neighboring understory. In addition, insect herbivore

and predator abundance and herbivory rates were higher in sunny patches than in shady patches (Lincoln & Mooney 1984, Louda & Rodman 1996, Sipura & Tahvanainen 2000, Richards & Coley 2007). Furthermore, light availability of a given patch within an ecosystem can affect plant antiherbivore defenses (Larsson *et al.* 1986, Mole & Waterman 1988, Koricheva *et al.* 1998), abiotic conditions that affect herbivorous insect behavior and growth rates (Stamp & Bowers 1994, Chase 1996), and activity level of predatory insects (Shelly 1982, 1984). In short, the influences on herbivorous insects can vary widely between sunny and shaded habitats. Here we investigate how food quality and predation differs between treefall gaps and the closed-canopy understory.

In many forests, gap formation by treefalls is a major part of the disturbance regime. The average rate of gap formation is about 1.5 percent of total land area per year (Brokaw 1982) in the lowland moist forest of Barro Colorado Island (BCI) Panama and about 1 percent in temperate eastern deciduous forests (Runkle 1982). On BCI this is about 1.56 km²/yr. While complete regeneration time for gaps can vary with gap size, a considerable portion of the forest area is at some open-canopy stage. Thus, the differences found in plant, herbivore, and predator interactions between gaps and understory are a common and widespread phenomenon.

We hypothesized that with increased resources in gaps, herbivores would be less resource-limited and more predator limited. Alternatively, in the understory, we predicted that herbivores would be more resource-limited than predator limited. To test this we combine field experiments with laboratory bioassays to answer the following questions: (1) Are there higher predation rates in gaps? (2) How do differences in food quality between gaps and understory effect herbivore growth and herbivory rates? (3) What is the combined effect of food quality and predation on herbivore behavior

and survival in gaps and understory? We focused our experiments on one of the most abundant understory shrub species on BCI, *Hybanthus prunifolius* (Violaceae, Schultze) (Croat 1978) and its herbivore *Zunacetha annulata* (Lepidoptera: Dioptidae).

METHODS

STUDY SYSTEM.—This study took place in the lowland moist forest of BCI, at the field station operated by the Smithsonian Tropical Research Institute, in the late rainy season of 2003. BCI has a wet season from May to November, and an average annual rainfall of 2.6 m. *Hybanthus prunifolius* is common in both treefall gaps and in the understory on BCI. Although *H. prunifolius* is shade-tolerant, when a light gap is formed, the plant drops and replaces the shade leaves with sun leaves that have 2.5 times greater photosynthetic rates (Kursar & Coley 1999). Thus, there is potential for differences in leaf quality between sun and shade leaves that can affect *Z. annulata*. *Zunacetha annulata* larvae feed primarily on *H. prunifolius* unless their populations reach outbreak levels (Wolda & Foster 1978). Adult *Z. annulata* generally oviposit eggs on *H. prunifolius* growing in gaps. The first two instars are gregarious, in clusters averaging 70 individuals. This allowed for easy field collections for experiments and bioassays.

LEAF QUALITY.—We measured leaf quality through bioassays, field herbivory rates and by quantifying toughness, water and nitrogen content, and specific leaf area (SLA).

First instar *Z. annulata* larvae were collected from the field and fed recently expanded sun or shade *H. prunifolius* leaves. *Hybanthus prunifolius* leaves live for 1 yr both in the sun and in the shade (Kursar & Coley 1999). Thus, differences in larval response to sun and shade leaves were not due to differences in leaf age. The larvae came from one large egg cluster found on a plant in medium light conditions along the trail. We placed 25 first instar larvae on sun leaves and 25 on shade leaves. One larva and one leaf were placed in individual containers and kept in a screened porch under ambient conditions (27°C). Initial leaf areas and larval weight were recorded before they were placed in containers. Every other day leaves were removed, remaining leaf area was measured, and a new field collected leaf was added. New leaves were collected from at least five plants from each environment and the plants collected varied every other day. We assigned leaves randomly to the larvae. Larvae were reweighed at 8 d, 14 d, and at pupation. From these bioassays, we calculated larval growth rates for the first 14 d, pupal weights, days to pupation, length of pupation, and leaf area consumed. We analyzed the data using an ANOVA or Mann–Whitney if the data did not pass the homogeneity of variance test.

Mature leaf herbivory rates were measured in the field in gaps and the understory. At the beginning of the rainy season, four of the most terminal leaves (recently matured) were tagged on 16 plants in gaps and 15 plants in the understory and previous herbivory was recorded. These plants were randomly selected and located throughout the old-growth forest of the island. We revisited the leaves at the end of the rainy season and recorded new herbivory.

Herbivory was measured by tracing the leaves and holes on a piece of paper in the field and measuring areas in the lab with a leaf area meter (LI-COR Biosciences, Lincoln, Nebraska). We used a *t*-test to determine if there was a significant difference in herbivory rates between habitats.

Leaf toughness, SLA, water content, and nitrogen content were quantified for sun and shade leaves. We sampled five leaves from five randomly selected plants growing in treefall gaps and the understory. These plants were different than those used in the herbivory study. We measured leaf toughness by averaging the weight needed to push a metal rod through the leaf using a Chatillon®, 516–1000 MRP push gauge (Chatillon, Largo, Florida). After we recorded toughness, leaf area, and wet and dry weights, the dried samples were pooled into sun leaves and shade leaves and run through a Wiley® Mill (Thomas Scientific, Swedesboro, New Jersey). We analyzed three samples of the ground batches of sun and shade leaves for nitrogen content using a Total Kjeldahl Nitrogen (TKN) digestion (Hach Company, Loveland, Colorado). Due to the variability of the digestion, we analyzed nitrogen content using a two-tailed paired *t*-test, pairing gap, and understory samples that were digested in the same batch. We analyzed leaf toughness, SLA, and water content using *t*-tests.

FIELD PREDATOR EXPERIMENTS.—We ran an enclosure experiment in the late rainy season of 2003 (29 October–12 November). We located nine paired gap and understory *H. prunifolius* plants, with members of each pair < 100 m apart. Enclosure cages were placed around one branch of each plant. The cages consisted of bridal veil 1 mm² diameter mesh suspended above a branch from a PVC pipe staked to the ground and a stiff wire loop (30 cm diameter) attached at the top of the pipe. This method held the material off the branch. We traced all the leaves on the branch to be enclosed for herbivory damage and then we placed eight third instar *Z. annulata* larvae on the terminal leaf of the branch. We sewed the material closed around the branch with larvae and applied Tanglefoot® to all access points to the branch to prevent ants from chewing through the bridal veil. We also placed eight more third instar larvae on the terminal leaf of an opposing uncaged branch on the same plant. We returned after 24 and 48 h and searched the plants for remaining larvae in and outside the enclosure. At the end of the experiment when we took down the cage, we traced the leaves to quantify new herbivory. We analyzed the leaf area consumed per larva per day using a paired *t*-test. We used an ANOVA to compare percent of larvae remaining per day in and outside enclosures (treatment effect) and between plants in gaps and in the understory (habitat effect). In the analysis we included enclosure pairs as a random factor and the values were not transformed. Predation rates between habitats were calculated as 100 minus the difference in the percent of the larvae remaining in the enclosures versus outside of the enclosures.

ESTIMATED LARVAL SURVIVAL.—Using the results from the field experiment and bioassays we calculated an estimate for larval survival. These calculations incorporated percent predation per day, the effects of food quality on the number of days to pupation, and survivorship to adulthood.

LARVAL BEHAVIOR.—We recorded time budgets and distance traveled by the larvae in the field predation experiments. We observed the larvae for 30 min and recorded larval activity every minute. Activities included eating, resting, traveling to other leaves, and searching (in which the larva was walking and moving its head back and forth). We recorded time budgets for the larvae placed on the open branch at the beginning of the experiments and for the remaining larvae after 24 h. All of the time budgets measurements were made at the same time of day at 0900–1200. We recorded time budgets in this manner for all pairs of plants in gaps and the understory within 1.5 h and in random order. Time budgets of larvae that were molting were excluded from the analysis. We tested if larvae behaved differently between gaps and understory using a MANOVA. The dependent variables tested were percent of time spent eating, searching, and traveling. We excluded the time spent resting from the analysis to increase independence between behavior categories.

In addition, we measured the distance traveled by the larvae everyday during the experiments. We measured the distance of each larva from the initial placement or previous known location to the current location at the time of census. The measurements followed the branches in the shortest most likely path the larva could have taken. We recorded the distance traveled after the 30-min time budgets, the next day (24 h) and on the second day (48 h). We used a Kruskal–Wallis test and analyzed each day separately.

RESULTS

LEAF QUALITY AND CATERPILLAR PERFORMANCE.—*Zunacetha annulata* larvae that were fed gap leaves had higher growth rates and ate less than larvae feeding on understory leaves (Table 1; $F_{1,39} = 151.2$ and Mann–Whitney U, $Z = -3.80$, $P < 0.001$, respectively). Larvae on gap leaves also had higher pupal weights, took fewer days to reach pupation than larvae on understory leaves (Mann–Whitney U, $Z = -4.32$ and -4.49, $P < 0.001$, respectively). Mortality was higher in larvae that feed on understory leaves (64% vs. 44%), although not significant ($\chi^2 = 1.087$, df = 1, $P = 0.30$). The main difference in mortality of larvae occurred during the pupation stage. There was 20 percent mortality of larvae before pupation in both treatments.

TABLE 1. *Bioassay results from* Z. annulata *larvae feeding on gap leaves and understory leaves of* H. prunifolius *in Panama.*

	Gap leaves	Understory leaves
Growth rates during first 2 wks (mg/d) **	0.123 ± 0.005	0.054 ± 0.003
Leaf area consumed (cm²)*	136 ± 5	211 ± 12
Days to pupation*	18.9 ± 0.4	25.0 ± 1.0
Pupal weight (g)*	0.084 ± 0.004	0.054 ± 0.002
Length of pupation (d)	8.38 ± 0.40	9.33 ± 0.24
Percent survival to adult	56%	36%

Asterisk indicates a significant difference between larvae feeding on gap and understory leaves (** ANOVA; *Mann–Whitney, $P < 0.01$).

TABLE 2. *Leaf quality characteristics and field herbivory rates of gap leaves and understory leaves.*

	Gap leaves	Understory leaves
N content (%/dry mass)*	3.26 ± 0.11	4.04 ± 0.08
Water content (%)	79.3 ± 0.5	78.8 ± 0.3
Toughness (g)	44.7 ± 5.9	17.4 ± 2.8
SLA (cm²/mg)*	292 ± 8	343 ± 10
Herbivory-		
In the field (%/day)*	0.170 ± 0.04	0.07 ± .02
In enclosures (cm²/day/larva)	3.24 ± 0.45	3.33 ± 0.37

Asterisk indicates a significant difference (*t*-test, $P < 0.05$).

However, 44 percent of the larvae on understory leaves died during pupation compared to 24 percent of the larvae on gap leaves. There was no difference in pupal weights between those that eclosed or died during pupation ($F_{1,23} = 1.36$, $P = 0.25$).

Hybanthus prunifolius leaves in gaps and the understory had different characteristics that affect food quality (Table 2). Leaves growing in gaps had a higher SLA ($t_{6.2} = 2.81$, $P = 0.03$) and lower nitrogen content than understory leaves ($t_2 = -4.04$, $P = 0.04$). Sun and shade leaves did not differ in toughness and water content ($t_{4.9} = -2.17$ and $t_{6.8} = -0.647$, $P > 0.05$, respectively). In the field, herbivory rates in gaps were significantly higher than in the understory ($t_{24.5} = 2.04$, $P = 0.05$, Table 2).

FIELD PREDATION EXPERIMENTS.—Larvae survival rates were higher in the enclosures. There was a significant treatment effect on the percentage of larvae remaining on the plants ($F_{1,8} = 16.6$, $P = 0.004$; Fig. 1). There were significantly fewer larvae remaining on gap plants than on understory plants ($F_{1,8} = 5.73$, $P = 0.04$; Fig. 1). However, there was no interaction between habitat and treatment on larvae remaining ($F_{1,8} = 1.11$, $P = 0.32$). The average percent predation per day was 26.5 in gaps and 13.8 in the understory (95% CIs of 14.2–30.8% and 3.8–20.4%, respectively).

Most larvae were removed without leaving any evidence; nonetheless, we found visual signs of predation on larvae outside and inside of the enclosure. These included finding the remains of a predator attack. We found three times as many larvae showing evidence of attack in gaps as compared to the understory outside the enclosures (8.8% vs. 2.7%). In addition, of the 12 larvae that died in enclosures on gap plants, three of them were from predator attack. The predators either attained access by chewing through the veil or in one case the larva was attacked through the veil and pieces were pulled though the mesh. The other causes of death of larvae in the enclosures were disease and drowning. Drowning occurred when the larvae crawled between the mesh and the stem or wire loop, water from heavy rains collected in these areas and the larvae were trapped. None of the four larvae that died in the understory enclosures were from predation. These direct observations of predation support our results (Fig. 1) of higher rates in gaps.
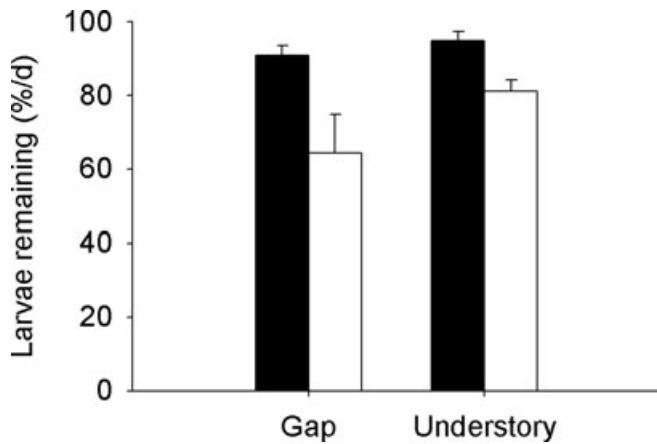
FIGURE 1. Mean percentage of larvae remaining per day inside (black bars) and outside (clear bars) of the enclosures on gap and understory plants (± SE). There were significant main effects of treatment and habitat (ANOVA, $P < 0.05$).

FIGURE 3. Distance traveled by larvae in gaps and in the understory after 30 min (day 0), on day 1 and on day 2 (± SE). Asterisks indicate significant differences in the distance traveled between larvae in gaps (clear bars) and in the understory (black bars; Kruskal–Wallis test, $P < 0.01$).

Herbivory in enclosures did not differ between gaps and understory ($t_8 = -0.19$, $P = 0.85$; Table 2). However, there was a marginal difference in the number of leaves with new herbivory between gap and understory (7.7 ± 0.8 and 9.9 ± 1.4 leaves respectively, $t_8 = -2.05$, $P = 0.07$). Herbivores sampled more leaves in the understory than in gaps.

LARVAL BEHAVIOR.—There were significant main effects of habitat (gap vs. understory) and time (first 30 min vs. after 24 h) on larval behavior (Wilks' Lambda 0. 745, $P = 0.034$ and 0.46, $P < 0.001$, respectively; Fig. 2). While there was no habitat effect on time spent
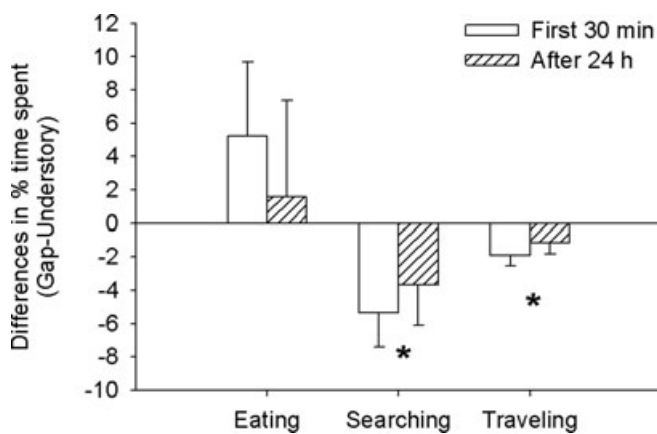

FIGURE 2. Differences between larval behavior in gaps and understory in the first 30 min and after 24 h of being placed on the plant (± SE). The y-axis is the percentage of time spent doing a certain behavior in gaps minus time spent in the understory. Thus, values above zero indicate more time was spent doing the behavior in gaps and below zero indicate more time doing the behavior in the understory. Asterisks indicate behavior patterns that were significantly different between gaps and understory at $P < 0.05$.
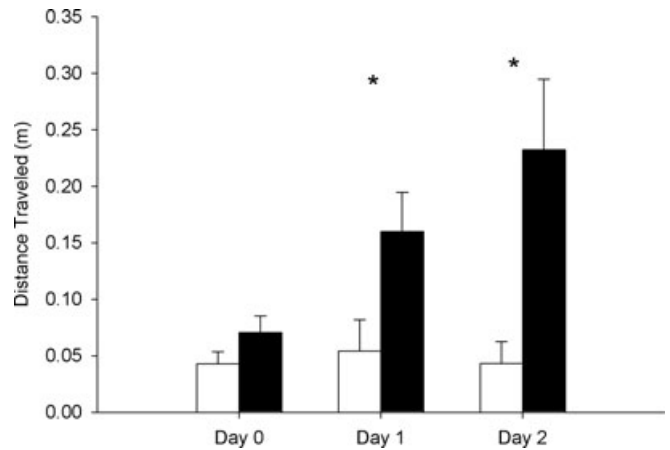
eating ($F_{1,31} = 0.049$, $P > 0.05$), larvae in the understory spent more time searching and traveling ($F_{1,31} = 5.68$ and 6.01, $P < 0.05$, respectively). In the first 30 min time budget, the larvae spent more time eating and searching than in the time budget 24 h later ($F_{1,31} = 8.79$ and 35.1, $P < 0.05$, respectively). There was no habitat by time interaction (habitat × time Wilks' Lambda 0.993, $P > 0.05$).

Larvae in the understory traveled greater distances than those in gaps (Fig. 3). There was no significant difference in the distance traveled in the first 30 min (Kruskal–Wallis, $\chi^2 = 2.76$, df = 1, $P = 0.10$). However, larvae traveled significantly greater distances in the following 2 d (Day 1, $\chi^2 = 22.4$, df = 1, $P < 0.001$; day 2, $\chi^2 = 10.5$, df = 1, $P = 0.001$).

ESTIMATED LARVAL SURVIVAL.—We estimated that the combined effects of food quality and predation rates should lead to lower larval survival in gaps than in the understory. We calculated the cumulative predation for larvae in gaps and the understory based on the duration of the larval stage (Table 1, days to pupation). When this predation measure was combined with the length of the larval stage and survivorship to adult determined in the feeding bioassays (Table 1), overall survivorship was calculated to be 0.22 percent in gaps and 1.02 percent in the understory.

DISCUSSION

Larvae that fed on *H. prunifolius* in gaps and in the understory experienced differences in potential predation and food quality. In gaps, where food quality and predation were higher, larvae were less active. In comparison, where food quality and predation were lower in the understory, larvae were more active.

Predation experiments using enclosures can be difficult to interpret because manipulations made to limit predator access to the larvae will also limit larvae from migrating off focal plants. However, combining the predation experiment with behavioral data helps clarify whether the missing larvae are from migration, predation, or both. We found multiple lines of evidence demonstrating that larvae in the understory migrate more than those in gaps. Behavioral observations showed that larvae in the understory spent more time traveling and went longer distances than those in the sun. Sipura and Tahvanainen (2000) also found significantly more migration in Chrysomelidae in the shade than in the understory. Therefore, we suggest that missing larvae in the understory are from a combination of predation and migration. In comparison, larvae in gaps did not show the same tendency for migration and we found more signs of predation. Thus, we suggest that missing larvae in gaps are primarily due to predation. Significantly more larvae missing in gaps suggest higher predation in gaps.

The higher survival in our understory treatments is consistent with results from previous studies done on BCI during the rainy season (Harrison 1987, Richards & Coley 2007). Harrison (1987) found 65 percent daily survival of *Z. annulata* larvae in gaps compared to 78 percent in the understory. These results are similar to our survival rates recorded for larvae outside the exclosures, 64 and 81 percent, respectively (Fig. 1). In addition, we estimated daily predation rates from the differences in survival of caged and uncaged larvae. These rates were 26 percent in gaps and 14 percent in the understory, which is consistent with predation rates found on artificial caterpillars, 18 percent in gaps and 12 percent in the understory (Richards & Coley 2007). Thus, independent studies with real and artificial caterpillars have found higher predation rates in the sun.

Although understory leaves had higher nitrogen content, larvae preformed poorly on understory leaves. These data and Harrison's (1987) data show that larvae grew 25 percent faster on gap leaves. Generally, herbivore growth rates are positively correlated with leaf nitrogen content (Mattson 1980). Therefore, other traits that we did not measure, such as chemical defenses, must be driving these differences in performance.

The differences in larval behavior between gaps and the understory reflect the differences in predation pressure and food quality. In gaps, leaves are of adequate quality for growth, which reduces the need for larvae to travel and search for higher quality leaves. In addition, higher predation pressure in gaps may also result in a reduction in larval activity as a means to decrease visibility to natural enemies. In comparison, poor food quality in the understory caused the larvae to be more active and sample more leaves in search of better quality food. Thus, the need to find better food apparently outweighed the increased visibility to natural enemies.

Wolda and Foster (1978) estimated larval survivorship for *Z. annulata* at 0.4 percent, which is similar to our estimates (gaps: 0.22%; understory: 1.02%). Our estimate for larval survivorship did not differ between habitats due to balancing effects of food quality and predation. Our estimates, however, do not account for predation on eggs and pupae. In addition, predation rates were measured for third instar larvae, however, predation rates often change through development with higher rates on earlier instars. Our estimates of survivorship are considerably lower than the results of Hawkins *et al.* (1997), in which they found 86 percent survivorship to pupation for tropical larvae. Our study examined a single species while Hawkins *et al.* (1997) summarized patterns in 11 tropical/subtropical studies including several holometabolous herbivore insects.

Adult *Z. annulata* prefer to lay eggs in gaps (Wolda & Foster 1978) where predation rates are higher. Similarly, Sipura and Tahvanainen (2000) found that the herbivores *Galerucella lineola* and *Phratora vitellinae* (Coleoptera: Chrysomelidae) preferred to oviposit on sun leaves in the field, even though predation was higher and sun leaves were a poorer food source than shade leaves. The authors suggested that ambient temperatures dictated adult preference. Abiotic differences between gaps and understory may contribute to the differences in oviposition preference of adults. However, Harrison (1987) found no temperature effects on *Z. annulata* growth rates. Thus, we suggest that food quality is driving oviposition preferences. There are likely other factors affecting survivorship not included in our estimates that can alter the magnitude of the differences between gaps and understory.

Light-gaps created by treefalls are reliable sources of habitat heterogeneity on the tropical forest floor. Many plant species have evolved traits to take advantage of these patches of high light (Denslow *et al.* 1990, Hubbell *et al.* 1999, Dalling *et al.* 2001), including *H. prunifolius* (Kursar & Coley 1999). *Hybanthus prunifolius* in gaps may be less defended because not only can they quickly replace biomass lost to herbivores, but also natural enemies help keep herbivores in check. We found evidence that predators limited larvae in the high light habitats of gaps, whereas the quality of food resources limited larvae in the shaded understory. These results support the hypothesis that herbivores experience greater predator limitations in gaps and greater resource limitations in the understory (Richards & Coley 2007). In addition, our findings are consistent with the prediction that predators have the greatest impact on herbivores in patches of high productivity (Hochberg & van Baalen 1998).

ACKNOWLEDGMENTS

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