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MORELLATO, L. P. C., AND H. F. LEITÃO-FILHO. 1996. Reproductive phenology of climbers in a southeastern Brazilian forest. Biotropica 28: 180–191.
OSUNKOYA, O. O. 1994. Postdispersal survivorship of north Queensland rainforest seeds and fruits: effects of forest, habitat and species. Aust. J. Ecol. 19: 52–64.
PARKER, R. E. 1975. Introductory statistics for biology. Edward Arnold, London, England.
PUTZ, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65: 1713–1724.
VAN DER PIJL, L. 1982. Principles of dispersal. Springer-Verlag, Berlin, Germany.
VÁZQUEZ-YANES, C., AND A. OROZCO-SEGOVIA. 1984. Ecophysiology of seed germination in the tropical humid forests of the world: a review. *In* E. Medina, H. A. Mooney, and C. Vázquez-Yanes (Eds.). Physiological ecology of plants in the wet tropics, pp. 37–50. Dr W. Junk, The Hague, The Netherlands.
WESTOBY, M., E. JURADO, AND M. LEISHMAN. 1992. Comparative evolutionary ecology of seed size. Trends Ecol. Evol. 7: 368–372.

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What's Up? An Experimental Comparison of Predation Levels between Canopy and Understory in a Tropical Wet Forest[1]

Key words: *herbivores; Peru; predation; top-down forces; tropical forest canopy.*

THE IMPORTANCE OF TOP DOWN–BOTTOM UP FORCES in explaining the distribution and abundance of herbivores has received considerable attention in the literature (Walker & Jones 2001). Bottom-up forces are hypothesized to affect herbivore populations through food limitation (Power 1992, Quinn *et al.* 1997, Farji-Brener 2001). In contrast, top-down forces are proposed to regulate herbivore populations through predators and parasites (Hairston *et al.* 1960). The relative importance of top-down and bottom-up forces is hypothesized to depend on the balance between the efficiency of prey consumption by predators and plant defenses (Coley 1983, Power 1992). Consequently, the importance of top-down or bottom-up forces can vary across habitats (McNaughton *et al.* 1989) and also within habitats; however, comparisons within habitats (*i.e.,* across vertical strata) have been largely ignored (Walker & Jones 2001).

In a tropical wet forest, the canopy and understory differ in physical structure, resource availability, and abiotic conditions (Yanoviak & Kaspari 2000), and thus offer an ideal situation for studying the relative importance of top-down and bottom-up forces within habitats. Comparisons, however, within habitats across vertical strata have primarily focused on resource (or bottom-up) limitation (Yanoviak & Kaspari 2000, Kaspari & Yanoviak 2001). Consequently, the relative importance of top-down forces controlling herbivore populations between forest canopy and understory is basically unknown. In this study, we experimentally tested whether or not predation levels differed between forest canopies and understory in a tropical wet forest.

Light for plant growth is considerably more limited in the forest understory compared to canopy habitats and thus the production of young leaves, which are a preferred food of herbivores (Coley 1983), is greater in forest canopies. Following this pattern, diversity and abundance of insect herbivores is greater in forest canopies than in the understory (Erwin 1982). How does greater number of herbivores and

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food resources in forest canopies affect herbivory rates? In an examination of seasonal variation in herbivore pressure across vertical strata in Panama, Barone (2000) found that for *Quararibea asterolepis*, adult trees in forest canopies had significantly greater numbers of herbivores than saplings in the forest understory but did not suffer greater levels of herbivory on young leaves. So, what's up? Lack of differences in herbivory damage between forest canopy and understory in *Quararibea*, despite large differences in herbivore numbers, may result from differences in quality of leaves with tree age, or be a result of greater predation pressure (top-down force) on herbivore populations in the canopy.

To test the relative importance of predation between forest canopies and understory, we placed artificial caterpillars on leaves in the two strata and compared predation levels. Because leaf damage can attract enemies of herbivores through chemical or visual cues (Agrawal 1998), we also examined the effect of leaf damage on predation levels by dividing these caterpillars between damaged and undamaged leaves. The release of volatile compounds that attract enemies to damaged leaves is, however, a short-term phenomenon (Agrawal 1998). Because we did not know when damage occurred on leaves used in this study, if differences exist in predation of artificial caterpillars between damaged and undamaged leaves, it is likely a result of predators using visual cues to find prey.

This study was conducted during May 2000 at ACEER, a tropical lowland wet forest site in the Peruvian Amazon (3°11′S, 72°53′W), 160 km downriver from Iquitos and 0.5 km upstream on the Sucusari river, a tributary of the Napo river. The site contains an extensive canopy walkway system that includes 14 tree platforms and walkways extending over 500 m distance. The majority of the walkway occurs at heights greater than 25 m (up to 37 m), providing access to leaves of several different canopy tree species, including *Apeiba membranacea*, *Anaueria brasiliensis*, *Brosimum rubescens*, *Buchenavia* sp., *Eschweilera coriacea*, *Guatteria elata*, *Hyeronima alchorneoides*, *Minquartia guianensis*, *Pouteria* sp., *Protium altsonii*, *Virola callophylia*, and *V. pavonis*. In addition, several kilometers of trails provide access to the forest understory where individuals of Arecaceae, Melastomataceae, Rubiaceae, and understory herbs are common.

To measure variation in predation pressure on herbivores between canopy and understory habitats, we made artificial caterpillars using modeling clay. Such models have been effectively used to estimate predation in various systems (Bayne & Hobson 1997, Rangen *et al.* 2000). These models do not provide an estimation of natural predation levels but they do serve as relative measures of predation across habitats (Martin 1987). Caterpillar models were uniform in length and width (*ca* 20 × 4 mm) between habitats. All caterpillars had a green body and yellow head. Caterpillars were modeled after Sphingidae (hornworms) and Brassolinae (owl butterflies), which represent common herbivores in tropical wet forests (T. Erwin, pers. comm.).

In canopy and understory habitats, 10 randomly selected locations were used for predation studies ($N = 20$ locations). At each location, we put ten caterpillars on the upper side of entire, simple leaves; five caterpillars were placed on damaged leaves (*ca* 25% herbivory) and five on undamaged leaves. Consequently, caterpillars were distributed between two treatments (damaged and undamaged) at each of the 20 locations. As we could not control for plant species used in both strata due to limitations of available trees in the canopy, we chose instead to place caterpillars on leaves that were similar in size and shape (*i.e.,* simple, entire leaves). Due to large differences in plant size between the two habitats, at any location, caterpillars were spread between more individuals in the understory. Caterpillars were distributed over a similar area (*ca* 15 m^2), however, in canopy and understory locations. At each stratum, locations were separated by *ca* 50 m. Twenty-four hours later, we noted the marks left by predators on the caterpillars. Depredation rate in damaged and undamaged leaves at each location was estimated as the proportion of caterpillars with predation marks. The identity of predators (birds, rodents, and ants) was determined by examining characteristics of the marks left on the caterpillars.

Variation in predation rates was examined using analysis of variance (ANOVA) models. Prior to analysis, we tested dependent variables for normality, and when necessary used an arcsine transformation to meet the assumptions of normality. We first examined differences in predation levels on damaged and undamaged leaves using a randomized block design with damage as the main effect and locations as blocks. We used this model as artificial caterpillars were placed on damaged and undamaged leaves in pairs at the 20 locations. Thus, predation on caterpillars in each of the treatment classes (damaged/undamaged) may have been influenced by location (block). We found no significant difference in predation of caterpillars on damaged and undamaged leaves ($F_{1,19} = 0.32$, $P = 0.85$). Similar predation levels between damaged (65.0% ± 7.38) and undamaged leaves (63.5% ± 7.85) suggest that damage does not serve as a visual cue for herbivore predators and is consistent with the dominance of ants as predators in this system (see below). Therefore, we combined data for damaged and undamaged leaves at a location and then examined the effect of vertical strata on predation levels using one-way ANOVA.

The percentage of caterpillars preyed upon was greater in the canopy than in the forest understory (77.3 ± 6.7 vs. 51.3 ± 7.3, respectively; $F_{1,18} = 5.04$, $P < 0.04$). Ants were the major predator on caterpillars (*ca* 90% of locations) in both canopy and understory habitats. Predation by birds (5% of locations) occurred only in forest canopy, while predation by rodents (20% of locations) occurred only in forest understory. Ant predators included *Crematogaster parabiotica*, *Camponotus femoratus*, and *Dolichoderus* sp. (based on observations in the field).

We found that predation levels measured were 25 percent greater in the canopy than in forest understory, suggesting that predation is relatively more important in forest canopies. Although rates here obtained do not reflect natural levels of predation, these kind of short-term studies likely provide reliable estimations of "relative" predation rates across study sites.

Greater rates of predation in the canopy support both the hypothesis that forest canopies are more N-limited than understory (Kaspari & Yanoviak 2001), and that the strength of top-down forces will increase with increasing primary productivity (Price *et al.* 1980). Additionally, this result also could explain the observations of similar herbivory levels between vertical strata despite the greater availability of young, palatable leaves in the forest canopy (Barone 2000). Chemical defenses and rapid leaf expansion during periods of low herbivore abundance are hypothesized to be the primary defense strategies of young leaves (Aide 1993). This study suggests that the third trophic level also serves to lower herbivory rates, but the relative importance of this indirect plant defense depends on vertical location of leaves within the forest.

If in tropical wet forests the relative importance of top-down and bottom-up forces differs between vertical strata at a local scale, understanding the dynamics of herbivore populations and herbivory rates should include canopy studies.

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AGRAWAL, A. 1998. Leaf damage and associated cues induce aggressive, ant recruitment in a Neotropical plant. Ecology 79: 2100–2112.

AIDE, T. M. 1993. Patterns of leaf development and herbivory in a tropical forest understory community. Ecology 74: 455–466.

BARONE, J. A. 2000. Comparison of herbivores and herbivory in the canopy and the understory for two tropical tree species. Biotropica 32: 307–317.

BAYNE, E. M., AND K. A. HOBSON. 1997. Comparing effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. Conserv. Biol. 11: 1418–1429.

COLEY, P. D. 1983. Herbivory and defense characteristics of tree species in a lowland tropical forest. Ecol. Monogr. 53: 209–233.

ERWIN, T. E. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. Coleop. Bull. 36: 74–75.

FARJI-BRENER, A. G. 2001. Why are leaf-cutting ants more common in early secondary forests than in old-growth tropical forests? An evaluation of the palatable forage hypothesis. Oikos 92: 169–177.

HAIRSTON, N. G., F. E. SMITH, AND L. B. SLOBDOKIN. 1960. Community structure, population control, and competition. Am. Nat. 94: 412–424.

KASPARI, M., AND S. P. YANOVIAK. 2001. Bait use in tropical litter and canopy ants. Evidence of differences in nutrient limitation. Biotropica 33: 207–211.

MARTIN, T. E. 1987. Artificial nest experiments: effects of nest appearance and type of predator. Condor 89: 925–928.

MCNAUGHTON, S. J., M. OSTERHELD, D. A. FRANK, AND K. J. WILLIAMS. 1989. Ecosystem level patterns of primary productivity and herbivory in terrestrial habitats. Nature 341: 142–144.

POWER, M. 1992. Top-down and bottom-up forces in food webs: Do plants have primacy? Ecology 73: 733–746.

PRICE, P. W., C. E. BOUTON, P. GROSS, B. A. MCPHERSON, J. N. THOMPSON, AND W. BOECKLEN. 1980. Interactions among three insect herbivores and natural enemies. Ann. Rev. Ecol. Syst. 11: 41–65.

QUINN, R., K. GASTON, AND D. BOY. 1997. Coincidence between consumer and host occurrence: Macrolepidoptera in Britain. Ecol. Entomol. 22: 197–208.

Rangen, S. A., R. G. Clark, and K. A. Hobson. 2000. Visual and olfactory attributes of artificial nests. Auk 117: 136–146.

Walker, M., and T. H. Jones. 2001. Relative roles of top-down and bottom-up forces in terrestrial tritrophic plant–insect herbivore–natural enemy systems. Oikos 93: 177–187.

Yanoviak, S. P., and M. Kaspari. 2000. Community structure and the habitat template: ants in the tropical forest canopy and litter. Oikos 89: 259–266.

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