

David Dilcher, Terry A. Lott

Florida Museum of Natural History
University of Florida
Gainesville, Florida 32611, U.S.A.

Paul R. Renne

Berkeley Geochronology Center
Berkeley, California 94709, U.S.A. and
Department of Earth and Planetary Science
University of California
Berkeley, California 94720, U.S.A.

Michael C. Wiemann

Center for Wood Anatomy Research
USDA Forest Service Forest Products Laboratory
Madison, Wisconsin 53705, U.S.A.

Duane Cozadd

Department of Geography
University of Tennessee
Knoxville, Tennessee 37996, U.S.A.

and

Orlando Vargas³

La Selva Biological Station
Organization for Tropical Studies
Puerto Viejo de Sarapiquí, Costa Rica

² Corresponding author. e-mail: shorn@utk.edu; Telephone: 865-974-6030.

³ Current address: Reserva Ecológica Bijagual de Sarapiquí, Apartado 35–3069, Costa Rica.

BIOTROPICA 35(3): 441–445 2003

Impact of *Atta colombica* Colonies on Understory Vegetation and Light Availability in a Neotropical Forest¹

ABSTRACT

We quantified patterns of vegetation removal and light availability above *Atta colombica* nests on Barro Colorado Island, Panama. Ants cleared vegetation less than 1 cm in diameter from an area of 77 m², and up to 3 m above ground level. Overall light availability 1.5 m above ground level was 49 percent greater at ant nest sites than at sites in undisturbed understory. These higher light levels fell within the range known to enhance growth of both shade tolerant and pioneer species.

Key words: *Atta colombica*; *Barro Colorado Island*; *light availability*; *tropical moist forest*; *understory structure*.

LEAF-CUTTING ANT COLONIES OF THE GENUS *ATTA* represent a potential source of disturbance within Neotropical forests that may favor selective establishment of some plant species. Compared to undisturbed tropical moist forest, areas above and immediately around *Atta* nest sites have higher light availability (Farji-Brener & Illes 2000), higher soil nutrient levels (Haines 1978), and less leaf litter (Garrettson *et al.* 1998, Farji-Brener & Illes 2000). The area immediately above an active *Atta* nest has been characterized as an understory gap (Farji-Brener & Illes 2000), and once colonies die or abandon a nest site,

¹ Received 30 December 2002; revision accepted 3 July 2003.

these gaps may provide conditions for recruitment differing from those in either canopy light gaps or intact understory (Garretson *et al.* 1998, Farji-Brener & Illes 2000).

Although nutrient availability in soil on *Atta* nests has been investigated extensively, there is currently much less information available on gap structure and the availability of light within understory gaps. The ground surface cleared above *Atta* nests has been measured many times (Fowler *et al.* 1986), but the size and shape of understory gaps above ant nests have not yet been quantified. Instantaneous readings of light levels taken with light meters suggest that light levels in understory gaps above *Atta* nest sites are higher than those in undisturbed understory (Farji-Brener & Illes 2000); however, it is difficult to estimate overall light availability from the scattered instantaneous measurements currently available. In this study, we quantified the density of understory vegetation and used hemispherical canopy photography to compare the light environment over *Atta* nests and in undisturbed understory.

The study took place in a lowland tropical moist forest on Barro Colorado Island, Republic of Panama. We studied six *Atta colombica* Guerin colonies and six understory sites that lacked evidence of both ant colonies and recent treefall gaps. We chose healthy, mature colonies at least 0.5 km away from the laboratory clearing and known to have been present in the same location for at least five years (H. Hertz, pers. comm.). We established understory plots near each of the six colonies in undisturbed forest in areas with similar aspect and slope.

The six *Atta* colonies had areas of disturbed soil in the shape of irregular ovals, with a mean cleared area of $77 \pm 6 \text{ m}^2$. Based on these dimensions, we sampled vegetation in $8 \times 10 \text{ m}$ areas at each nest and each understory site. On ant nests, the long and short axes of the sampling area were oriented to match the shape of the area of disturbed soil. In each sampling area, we sampled stem densities in three different diameter classes: herbs and seedlings (<1 cm), shrubs and saplings (1–5 cm), and small trees (5–10 cm). Diameter was measured at 1.33 m (diameter at breast height; DBH) for plants taller than 1.33 m. For plants shorter than 1.33 m, diameter was measured at the midpoint of the largest ramet. Herb and seedling densities were measured using four 1 m^2 quadrats placed randomly within the 80 m^2 sampling area. Shrub and sapling densities were measured using four 9 m^2 quadrats placed randomly within the sampling area, and small tree densities were measured in four equal 20 m^2 ($4 \times 5 \text{ m}$) quadrats.

We then estimated foliage density from 0 to 5 m above the soil surface at ten randomly chosen points in each sampling area using a telescoping rod. At each sampling point, we extended the rod to a height of 5 m, and each time the rod encountered a leaf, stem, or branch, the height of the encounter was recorded to the nearest 0.5 m.

Finally, we used hemispherical canopy photographs to estimate the photosynthetically active radiation (PAR) reaching the understory at each of the 12 sites. We took black-and-white photographs using a 35 mm camera with an 8 mm fisheye lens mounted 1.5 m above ground at the center of each site. Photographs were taken on overcast days and canopy/sky contrast was enhanced by using of a red filter (Whitmore *et al.* 1993). Photographs were scanned and analyzed with the Hemiview 2.1 canopy analysis software (Delta-T Devices, Inc.). We used the Global Site Factor calculated for each photograph by Hemiview as an estimate of the fraction of full sunlight penetrating to the understory. Because understory gaps are thought to particularly enhance penetration of low angle and reflected light (Connell *et al.* 1997), we used the Direct and Indirect Site Factors calculated by Hemiview to separately estimate the fraction of direct and indirect insolation reaching the understory.

Data on stem and foliage densities were checked for normality and homogeneity of variances and transformed when necessary. Percentage data obtained from hemispherical photography were arcsine-square root transformed prior to analysis. After transformation, all data met requirements of parametric analyses for normality and homogeneity of variances, and mean values for each measurement taken at the six nest and six understory sites were compared using a *t*-test.

The density of plants less than 1 cm DBH differed significantly between ant nest and understory sites ($P < 0.001$), with nest sites having approximately one-fifth the density of plants found in understory sites (Table 1). Although densities of larger plants were also somewhat lower, these differences were not statistically significant. Foliage density from 0 to 5 m above the soil surface was also much lower over *Atta* nests than in undisturbed understory. Foliage density 0 to 1 m above ground level on ant nests was at least ten times lower than in undisturbed understory, and was significantly lower up to 3 m above ground level (Table 2).

The amount of light reaching the forest understory differed significantly between *Atta* nest and

TABLE 1. Density of plant stems (number per m²) in three size classes found on *Atta* nest sites and in adjacent understory on Barro Colorado Island, Panama. Mean values are \pm SD (N = 6).

Size class (cm DBH)	Ant nest	Understory	Significance level ^a
<1	6.58 \pm 1.26	30.54 \pm 3.92	$P < 0.001$
1–5	0.26 \pm 0.26	0.47 \pm 0.18	$P = 0.170$
5–10	0.066 \pm 0.047	0.119 \pm 0.046	$P = 0.103$

^a *t*-test.

understory sites by all measures (Table 3). Direct, indirect, and total PAR levels were all significantly greater over ant nests than at understory sites (Table 3). At nest sites, we estimated that 12.4 percent of available sunlight from all sources reached the understory, compared to 8.3 percent of available sunlight at understory sites. Ant nests thus received about 49 percent more sunlight than adjacent understory.

Our results confirmed that *Atta* colonies create understory gaps that reach up to 3 m above ground, and significantly increase understory light levels in tropical forest. Ants may generate such gaps by harvesting leaves for fungus culture, by unselectively cutting vegetation above the nest site prior to mating flights (Moser 1967, Waller 1986), or by burying seedlings beneath the large amounts of soil excavated from underground chambers (Autuori 1947). Ant colonies had measurable effects only on small plants of less than 1 cm DBH and only on a relatively small area, averaging 77 m²; however, within this small area, light levels were increased by 49 percent over those in adjacent forest, a substantial subsidy for seedlings growing in forest understory with low light availability.

Connell *et al.* (1997) have suggested that tree seedlings show enhanced growth in understory gaps primarily because of increased low-angle and reflected light, and as expected, indirect insolation was significantly greater at *Atta* nest sites (Table 3). Our data, however, indicate that direct insolation was enhanced by a similar amount. Removal of leaf layers close to the ground should increase direct insolation to some extent, but the increase observed in this study is hard to reconcile with simulations suggesting that most light is absorbed in the upper canopy layers (Wirth *et al.* 2003). We propose that two other processes may account for increased transmission of direct light at ant nest sites. First, direct insolation may be increased not only by removal of understory leaves, but by harvesting leaves from the canopy above the nest site, which is known to increase light transmission and the frequency of sunflecks (Wirth *et al.* 2003). Second, *Atta* queens are known to preferentially establish new colonies in light gaps (Jaffe & Vilela 1989, Vasconcelos 1990) and it is possible that the greater availability of direct sunlight over ant nests is a legacy of incomplete canopy closure in old gaps. We did note similarities between nest sites and old gaps on the Hubbell–Foster forest dynamics plot, including evidence of fallen tree trunks nearby and lower densities of large saplings than in understory, but were not able to establish a clear connection between our ant nests and old gaps.

The characteristics of *Atta* nest sites suggest that they represent a very different set of opportunities for regeneration than either undisturbed understory or open-sky treefall gaps. Although this study measured only relative light availability rather than absolute illuminance, at least one study has shown that an increase in relative light availability from 6 to 10 percent increased growth rates of both shade tolerant

TABLE 2. Vegetation contacts per sample point in five 1 m intervals above ground level. Mean values are \pm 1 SD (N = 6).

Height (m)	Contacts per sample point		Significance level ^a
	Ant nest	Understory	
0–1	0.067 \pm 0.033	0.917 \pm 0.170	$P < 0.001$
1–2	0.050 \pm 0.022	0.600 \pm 0.146	$P < 0.005$
2–3	0.100 \pm 0.037	0.317 \pm 0.087	$P < 0.05$
3–4	0.250 \pm 0.152	0.333 \pm 0.088	$P = 0.65$
4–5	0.200 \pm 0.103	0.367 \pm 0.105	$P = 0.29$

^a *t*-test.

TABLE 3. Total, direct, and indirect light availability estimated from hemispherical canopy photographs taken at 1.5 m above *Atta* nest sites and undisturbed understory sites on Barro Colorado Island, Panama. Mean values are \pm 1 SD (N = 6).

Light source	Percent of full sunlight		Significance level ^a
	Ant nest	Understory	
Total	12.4 \pm 2.6	8.3 \pm 1.4	$P < 0.01$
Direct insolation	11.6 \pm 2.5	7.9 \pm 1.4	$P = 0.01$
Indirect insolation	11.5 \pm 2.2	7.6 \pm 1.5	$P < 0.01$

^a *t*-test.

and light-demanding tropical tree species (Agyeman *et al.* 1998), suggesting that ant colonies may potentially enhance recruitment for many tree species. We conclude that the relationship between *Atta* colonies and seedling regeneration in tropical forests is worthy of additional study to determine if environmental conditions on abandoned nests enhance recruitment of a wide range of species or if some plant species have adapted to specialize in exploiting this favorable, though transient, regeneration niche.

We wish to thank the staff at the Smithsonian Tropical Research Institute for their assistance in all phases of this study. Field assistance was provided by H. Hertz, S. Hilger, and M. Panger. P. van der Meer contributed comments helpful in designing the study. J. Utley provided access to equipment used for digitizing photographs, and J. Denslow permitted us to use photographic equipment and software for analyzing hemispherical photographs. Helpful comments by A. Farji-Brener and R. Wirth improved the manuscript. Financial support was provided by grants from the Louisiana State Board of Regents and the UNO College of Sciences. We wish particularly to thank J. King, UNO Dean of Sciences, for his continuing interest in and support of this research.

- AGYEMAN, V. K., M. D. SWAINE, AND J. THOMPSON. 1998. Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *J. Ecol.* 87: 815–827.
- AUTUORI, M. 1947. Contribuição para o conhecimento do saúva (*Atta* spp.). (IV.) O saúveiro depois da primeira revoada (*Atta sexdens rubropilosa* Forel 1908). *Arq. Inst. Biol. São Paulo* 13: 137–148.
- CONNELL, J. H., M. D. LOWMAN, AND I. R. NOBLE. 1997. Subcanopy gaps in temperate and tropical forests. *Aust. J. Ecol.* 22: 163–168.
- FARJI-BRENER, A. G., AND A. E. ILLES. 2000. Do leaf-cutting ant nests make “bottom-up” gaps in Neotropical rain forests?: A critical review of the evidence. *Ecol. Lett.* 3: 219–227.
- FOWLER, H. G., V. PEREIRA-DA-SILVA, L. C. FORTI, AND N. B. SAES. 1986. Population dynamics of leaf-cutting ants: A brief review. In C. S. Lofgren and R. K. Vander Meer (Eds.), *Fire ants and leaf-cutting ants: Biology and management*, pp. 146–158. Westview Press, Boulder, Colorado.
- GARRETTSON, M., J. F. STETZEL, B. S. HALPERN, D. J. HEARN, B. T. LUCEY, AND M. J. MCKONE. 1998. Diversity and abundance of understory plants on active and abandoned nests of leaf-cutting ants (*Atta cephalotes*) in a Costa Rican rain forest. *J. Trop. Ecol.* 14: 17–26.
- HAINES, B. L. 1978. Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. *Biotropica* 10: 270–277.
- JAFFE, K., AND E. VILELA. 1989. On nest densities of the leaf-cutting ant *Atta cephalotes* in tropical primary forest. *Biotropica* 21: 234–236.
- MOSER, J. C. 1967. Mating activities of *Atta texana* (Hymenoptera, Formicidae). *Insect. Soc.* 14: 295–312.
- VASCONCELOS, H. 1990. Habitat selection by the queens of the leaf-cutting ant *Atta sexdens* L. in Brazil. *J. Trop. Ecol.* 6: 249–252.
- WALLER, D. A. 1986. The foraging ecology of *Atta texana* in Texas. In C. S. Lofgren and R. K. Vander Meer (Eds.), *Fire ants and leaf-cutting ants: Biology and management*, pp. 146–158. Westview Press, Boulder, Colorado.
- WHITMORE T., N. BROWN, M. SWAINE, D. KENNEDY, C. GOODWIN-BAILEY, AND W. GONG. 1993. Use of hemispherical photographs in forest ecology: measurement of gap size and radiation totals in a Bornean tropical rain forest. *J. Trop. Ecol.* 9: 131–151.
- WIRTH, R., H. HERZ, R. J. RYEL, W. BEYSCHLAG, AND B. HÖLDOBLER. 2003. Herbivory of leaf-cutting ants: A case study on *Atta colombica* in the tropical rainforest of Panama. Springer-Verlag, Berlin, Germany.

Helen M. Hull-Sanders² and Jerome J. Howard³

Program in Conservation Biology
Department of Biological Sciences

University of New Orleans
New Orleans, Louisiana 70148, U.S.A.

² Present address: Department of Entomology and Plant Pathology, Auburn University, Auburn, Alabama 36849, U.S.A.

³ Corresponding author. e-mail: jjhoward@uno.edu
