SHORT COMMUNICATION

Dispersal of *Miconia argentea* seeds by the leaf-cutting ant *Atta colombica*

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While leaf-cutter ants are thought to collect mainly vegetative plant material, they have also been observed collecting seeds or fruit parts on the forest floor (Alvarez-Buylla & Martínez-Ramos 1990, Kaspari 1996). For example, leaf-cutter ants have been observed carrying considerable numbers of *Brosimum alicastrum* Sw. and *Cecropia* spp. seeds into their nests (Wirth 1996) and Leal & Oliveira (1998; *pers. comm.*) found them foraging on the fruits and seeds of 19 different species of Brazilian cerrado vegetation, including six *Miconia* species. Under some circumstances, seed removal and relocation by leaf cutter ants might even be sufficient to affect local recruitment patterns of trees. For example, in Costa Rica, *Atta cephalotes* can remove all fallen fig fruit from beneath a *Ficus hondurensis* crown in a single night (Roberts & Heithaus 1986), while in Venezuela, seedling recruitment of the savanna tree *Tapirira velutini-folia* was positively associated with the seed harvesting and seed cleaning activities of the ant *Atta laevigata* (Farji Brenner & Silva 1996).

Clearly leaf-cutter ants may be important seed predators and secondary dispersers of small seeded species in tropical forests, just as are litter ants (Byrne & Levey 1993, Horvitz & Schemske 1994, Kaspari 1993, Levey & Byrne 1993, Perry & Fleming 1980). Although non-foliar plant material, such as fruits, flower parts and fig stipules can represent *c.* 30% of the total annual biomass intake of an *Atta colombica* (Guerin) (Hymenoptera: Formicidae) leaf-cutter ant colony (and even up to 50% during the dry season)(Wirth *et al.*

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1997), the impact of this behaviour on the vegetation has been little studied.

Herein, we report observations that the leaf-cutter ant *Atta colombica* not only alters the distribution pattern of fallen fruits of the tree *Miconia argentea* (Sw.) DC. (Melastomataceae), but that, on occasions, it also removes ripe undispersed fruit from within the canopy. *Miconia* is a common pioneer tree on BCI, reproductive from 10–40 cm DBH. From March to July it produces numerous 2–4 mm fleshy berries each containing 1–80 tiny seeds (Dalling *et al*. 1998). Seeds are primarily dispersed by birds, monkeys and coatis (Hladik & Hladik 1969).

Throughout the peak *Miconia* fruiting period from mid-April to late May 1994 we recorded the activity of two *Atta colombica* colonies (hereafter A and B with nest areas of 60 m^2 and 40 m^2 respectively) at the periphery of the laboratory clearing on Barro Colorado Island (BCI), Panamá. Activity measurements were made both day and night at 2-h intervals beginning surveys at 06h00 and ending at 06h00 the following day (control measurements made at 30 min and 1 h intervals gave similar results). Foraging rates were measured by counting ants laden with *Miconia* fruits and other forage material passing a fixed point close to the entrance hole of each active foraging trial. At each sample period laden ants were counted for 2 min (instead of conventional 1 min e.g. Hodgson 1955; Rockwood 1975, 1976) to account for temporal variability of ant activity on the trails. At colony A 24-h counts were made on 4 d, and at colony B on 6 d. The total daily nest input (Table 1) was estimated by summing the calculated hourly vegetation inputs for each foraging trail. On additional days (Table 1) we used regression estimates of daily foraging rates based on measurements made at the known peak period of foraging activity for the colony; these have recently been demonstrated to correlate very strongly with measured and calculated total daily intake rates for leaves and non-green plant parts (r^2 > 0.97 both colonies; Wirth *et al*. 1997).

Ants selectively harvested ripe *Miconia* fruit; we only occasionally observed ants harvesting green immature fruit. The foraging area for both neighbouring colonies were four or five, 15–20 cm DBH trees. For colony A, fruits were collected throughout the 3-wk period of peak fruit production from late April to mid May, while we observed fruit collection at colony B over a 6-wk period from mid April to late May. Although these ants were estimated to collect large numbers of fruit (Table 1; colony A estimated mean = 1470 fruits per day and Colony B estimated mean = 3110 fruits per day) only a small proportion (2%) of their total estimated foraging effort was spent collecting *Miconia* fruit.

We observed ants collecting fruits from both the canopy and from fallen infructescences beneath the crown. Two-minute counts made over one day at the base of the trunk of three *Miconia* trees indicated that ants can remove up to an estimated 1700 undispersed fruits/day from the canopy of a single tree. Although we have seen leaf cutters collecting fruits from the crown every

Table 1. Estimated daily inputs of *Miconia* fruits and leaf fragments into two *Atta colombica* nests. Fruit collection and the total collection of all plant material was observed over 20 d at colony A, and 49 d at colony B.

Date	Maximum input rate	Daily input *Miconia*	Daily input All forage	*Miconia* (%)[2]
Colony A	(fruits/min)			
25 April*	10	3 420	76 370	4.48
2 May†	2.5	690	111 760	0.62
4 May†	1.5	390	-	-
5 May*	8.5	2 460	–	–
8 May*	3	930	119 835	0.78
15 May*	3.5	900	148 365	0.61
Daily average (SE)		1 470(490)		1.6 (1.9)
Estimated total[1]		28 400		
Colony B				
11 April†	5	1 250	273 540	0.46
18 April†	8	2 610	204 585	1.28
25 April*	7	1 980	204 450	0.97
2 May*	10	4 590	187 740	2.44
4 May†	17	8 500	–	–
8 May*	15	6 590	161 565	4.08
15 May*	8	2 070	242 595	0.85
22 May*	2	390	13 365	2.92
29 May*	0.5	30	11 100	0.27
Daily average (SE)		3 110(1 180)		1.7 (1.3)
Estimated total[1]		136 200		

*24-h count made.
†Daily input estimated from a single 2-min count at the time of peak foraging activity.
[1]Estimated totals over the observation period were derived from calculated daily values.
[2]Percent of total forage items that were *Miconia* fruit.

year from 1993 to 1997, foraging rates from the canopy appear to vary greatly between days and between trees, and much more detailed observations will be needed to quantify the relative contributions of undispersed versus fallen fruit as forage sources. Future studies should also investigate how the activities of other frugivores such as mantled howler monkeys (*Alouatta palliata*) and white-throated monkeys (*Cebus capucinus*) that often throw down whole *Miconia* infructescences (Hladik & Hladik 1969) might affect leaf-cutter foraging patterns, or the extent to which leaf-cutters compete directly with vertebrate frugivores for ripe fruit in the canopy.

To examine whether *Miconia* seeds survive passage through the nest, we collected fresh samples of nest refuse deposited on the soil surface at colony 'A'. We placed a plastic sheet over the existing refuse mound and collected all fresh refuse over a period of 3 h on 18 d between late April and early July 1994. Each daily sample was thoroughly mixed, and a 7-g (fresh weight) subsample was spread evenly over the surface of a germination flat containing moist sand. Flats were placed in a screened growing house (*c.* 20% full sun) and emergent seedlings were removed and counted weekly over the following 6 wk.

Nest refuse contained a mean of 330 *Miconia* germinable seeds/g fresh weight refuse (SE = 110) between 14 May and 10 June (during which >95% of all

seedlings were recorded). A peak of 1080 seeds/g of refuse was reached on 15 May, and declined to zero by 17 July, *c*. 1 mo after the end of the fruiting season (Figure 1).
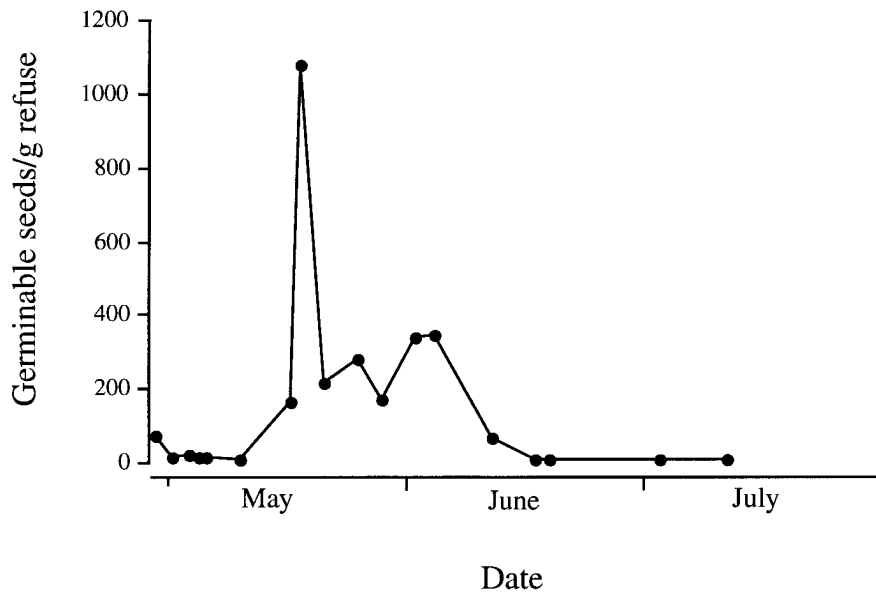

Figure 1. Density of *Miconia* seeds in refuse from Colony A collected through the fruiting season.

To determine the germinability of individual seeds in the refuse we used a stereoscope to extract a total of 146 seeds from samples taken on five consecutive days in late May, and compared germination with 300 seeds extracted from eight passively dispersed mature fruit collected beneath the tree crown. Seeds were placed in petri-dishes in a growth chamber (12 h dark at 25 °C; 12 h at 60 μmol m^{-2} s^{-1}, red : far-red 1.65, at 30 °C), and germinants counted weekly for 10 wk. Germination of seeds from refuse remained relatively high (73%), but was significantly lower than seeds from freshly collected fruits (84%) (Yates' corrected $\chi^2 = 6.38$, df $= 1$, P < 0.05). A recent study by A. G. Farji-Brenner & C. Medina (*pers. comm.*) indicates that *Miconia* seeds remain viable in the refuse for several months after their deposition; sampling similar *Atta colombica* nests on BCI 3 mo after the end of the *Miconia* fruiting season, they found seven times higher densities of germinable *Miconia* seeds around the nest than in adjacent forest soil.

During a recent survey, leaf-cutting ant colonies on BCI were found almost exclusively within 750 m from the edge of the laboratory clearing (Wirth 1996). Here, *Atta colombica* appears to be one of the principal seed dispersal agents of *Miconia argentea*, removing many fruit from within and beneath the crown, and depositing the seeds in the refuse pile beside the nest. *Atta colombica* may produce a more highly aggregated seed distribution pattern than other potential dispersers of this species (Dalling *et al.* 1998) and may therefore negatively

affect the fitness of this pioneer tree as it limits opportunities for seeds to encounter gaps. However, dispersal by leaf-cutters may be more advantageous than first appears. Firstly, fruits may be moved long distances from fruiting trees to ant nests (up to a maximum of 100 m for colony B), and some, perhaps significant proportion of fruits are discarded along the trail. Lugo *et al.* (1973), for example estimated that 30% of leaf fragments cut by *Atta colombica* do not reach the nest. The same fate may occur to fruits removed. Secondly, we did not examine the fate of seeds after entering the refuse pile. Some seeds may be removed by litter ants, and secondarily dispersed, albeit short distances, or washed out of the loosely consolidated refuse and re-deposited over a wider area following heavy rain. Finally, although *Miconia* seedlings have not been observed on extant nests, abandoned nest sites may be excellent sites for the regeneration of this small-gap specialist tree (Brokaw 1987).

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