

trails that carry leaves showed that soldiers do contribute to leaf collection. While the workers moved more leaves overall because they were more abundant, the soldiers were the dominant ants involved in moving obstacles. These findings suggest that the function of clearing obstructions is assigned primarily to the soldiers.

Perhaps in times of relative safety for the nest, a certain number of soldiers may be allocated to other functions, such as collecting leaves or moving obstacles. The additional help on the foraging trails would increase the productivity of the nest and thus increase fungal growth for food. Further testing by presenting a danger to the nest and measuring changes in soldier behavior or leaf biomass col-

lected could address this idea. Why our findings differ from those of Weber (1966) is not yet clear. It's possible that the nests he observed were already in a state of emergency, either from disturbances created by himself or by other unknown factors.

LITERATURE CITED

- Stevens, G. C. 1983. *Atta cephalotes*. In *Costa Rican Natural History*, ed. D. H. Janzen, 688-91. Chicago: The University of Chicago Press.
- Weber, Neal A. 1966. Fungus-Growing Ants. *Science*. Aug. 5. 587-599.

SELECTION OF GAP VERSUS SHADE LEAVES BY *ATTA CEPHALOTES* IN CORCOVADO NATIONAL PARK, COSTA RICA

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Abstract. Gap colonizing tree species invest less in chemical defense and may therefore be preferred by leaf cutter ants. We tested this idea using leaf pieces from gap and shade tree species, noting which were taken to the colony nest. As expected, the ants preferred gap species over shade species selecting them as often as they selected leaves from the tree they were currently harvesting. (TCB)

INTRODUCTION (TCB)

Leaf cutter ants (*Atta cephalotes*) are sustained by fungal gardens raised on leaf cuttings. The selection of food leaves may be important to the health of the fungus, and thus the ants should show preferences among plant species. The exact criteria used by the ants in choosing a tree are unknown, but trees with fewer chemical defenses may be preferred. Gap colonizing plants invest less in chemical defense than shade tolerant understory species, and are often preferred by herbivores (Coley 1983).

We hypothesized that leaf-cutter ants would prefer the leaves of gap colonizing species to those of shade tolerant ones. We predicted that more of the gap than the shade leaves would be taken back to the nest when presented to the ants on their foraging trails.

METHODS (JMH)

We observed a leaf cutter ant trail on the Rio Claro Trail in Corcovado National Park, Costa Rica, from 1500 to 1800. This ant trail was coming from a tree, the foliage of which we had observed the ants harvesting. We collected leaves of the species being harvested, and also from trees pre-

sumed to be gap-colonizing species (found at the edge of a field) and trees found in the forest understory. We did not know if the species being harvested was a gap-colonizing or a shade species. Because of the difficulty in identifying these trees to species, we referred to them by letter labels (Table 1).

To determine how readily each species would be harvested, we placed a pile of five leaf pieces of that species in the center of the trail. Attempting to offer pieces which were similar in size and shape to ant-weight pieces, we tore the leaves into approximately 1cm² pieces. We had observed that the ants seemed less likely to carry pieces made with scissors or a hole punch, perhaps because a smoother edge is more difficult to grasp. We recorded the fate of each piece: ignored, cleared from the trail, or taken to the nest. We assumed that the piece was being taken to the nest if it was carried >25 cm from the pile in the direction of the nest. We watched each pile until all five pieces were carried away, or until the ants were ignoring all remaining pieces. We considered pieces to be ignored if (a), ten ants consecutively had investigated them but not picked them up, or (b), no ants had investigated them for one minute. We completed 10 replicates of the species

being harvested, and 2 replicates of each of the other species.

We assumed that the species which the ants were already harvesting would be accepted readily by them in our experiment, and so the data from this species were used as a control against which we could compare harvesting of the other ten species.

RESULTS (JJS)

We tested for differences in leaf preference among gap species, understory trees, and the tree being harvested (Table 1). Ants took the leaf parts of gap species more frequently than those from understory (shade) trees ($\chi^2=12.70$, $p<.005$). The ants also preferred leaves from the trees being harvested over those from the shade trees ($\chi^2=14.03$, $p<.005$). However, the ants exhibited no preference between gap leaves and those from the tree being harvested ($\chi^2=0.04$, $p>.5$). We could not statistically determine if there were species preferences within each category due to an inadequate number of replicates of each species ($n=2$). One gap plant, a species of Piperaceae, was rejected at every trial (Table 1).

Species	Category	Taken	Not Taken
A	gap	0	10
B	gap	7	3
C	gap	9	1
D	gap	3	7
E	gap	3	7
F	shade	0	10
G	shade	3	7
H	shade	0	10
I	shade	1	9
J	shade	2	8
K	harvested	23	27

DISCUSSION (TCB, JJS)

As hypothesized, the ants from the colony we studied preferred leaf pieces from gap colonizers rather than shaded understory trees. We infer that the gap species are more palatable to the ants, perhaps because of chemical and physical differences. Gap species allocate the majority of their resources to rapid growth and reproduction; they have fewer defensive chemicals in their foliage. Additionally, they invest less in thickening of leaves and stems, resulting in physically weaker leaves. Shade tolerant species grow more slowly, investing more in physical and chemical defense (Coley 1983).

We originally expected that the ants would most prefer pieces from the species they were foraging on at the time of the study. However, there was no difference between the number of pieces brought back to the nest from gap or the currently harvested species. There are two reasons why this may be. The first is simply that we handled the leaves; the pieces were not cut by the ants, and had no chemical cue signaling them to be taken. The second may be that rather than preferring the harvested species less than expected, they prefer gap species more. Irrespective of which species is currently being harvested, the ants will take leaves from gap species as readily as leaves from the harvested species. This implies that they prefer gap species most highly of all. This could be further tested by offering the ants a direct choice between the two leaf types.

These results further questions concerning leaf preferences by ants: if the ants prefer gap species so strongly, why do they forage on other species? Perhaps other factors such as heat stress resulting from exposure to direct

sunlight limit the ants' utilization of gap resources.

Even if chemical defenses are distributed evenly throughout an individual plant, sun leaves are smaller and thicker and may be preferred by the ants as a better resource for the fungus. If these sun leaves are indeed better for cultivating the fungus on which the ants depend, this may explain why ants climb to the tops of trees to harvest leaves, as they have been observed to do.

It is likely that several leaf attributes contribute to leaf selection by leaf-cutter ants, e. g., nutrient content, toughness, and chemical defenses. The preference we found for gap

species may be due to one or more of these attributes. The effects of each attribute could be tested in more detail by offering sun and shade leaves from the same tree, and offering leaves of differing ages or nutrient content. Future research may reveal that all of the mentioned factors play a part in leaf selection by these ants.

LITERATURE CITED

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