stage classes reflect differences in nitrogen dynamics. Initially, data in Figure 1 do not seem to support the hypothesis that cotyledon nitrogen concentration decreases with cotyledon age. There is a decrease in nitrogen concentration from the first to the second stage class, a large increase from the second to the third and fourth, and another decrease to the final stage class. A comparison of Figure 1 to Figure 2 shows that the increase in cotyledon nitrogen concentration from stage class 2 to 3 correlates with the appearance of roots. The young *Pentaclethra* tree may be either taking up nitrogen from the soil through its newly formed roots, taking up nitrogen-fixing rhizobia through its newly formed roots, or both. The absence of root nodules on plants used in the study indicates that rhizobia were not fixing nitrogen in the samples (Graham and Swenson 2001), suggesting that the seedlings were instead taking up nitrogen through their newly formed roots.

After this increase in nitrogen concentration with the root formation, cotyledon nitrogen concentration appears to decrease as root: shoot ratio decreases (Fig. 2), supporting the idea that a growing plant demands more nitrogen. Nitrogen appears to be taken away from the cotyledon and is probably invested into plant tissue. In addition, the cotyledons appear to be a temporary pool for nitrogen coming in through the roots. Perhaps by the time roots germinate, cotyledon nitrogen concentration is low in comparison to that of the soil, thus the potential difference for nitrogen diffusion is increased by the nitrogen deficient cotyledon tissue. Future study could investigate the ways in which *Pentaclethra* seedling-shoot-and-leaf-nitrogen concentration vary with cotyledon nitrogen concentration to determine total nitrogen allocation patterns for the seedlings. Further research into nitrogen allocation patterns for *Pentaclethra macroloba* may help explain its characteristic low levels of seed predation and its dominance of nutrient poor soils in the Neotropics.

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Preliminary exploration of the relationship between *Ficus colubrinae* and *Atta cephalotes*

Daniel M. Braden and Nicholas A. Friedenberg

Abstract: *Ficus* inflorescences perform two functions critical to the trees' reproduction; by providing a breeding ground for a symbiotic species of cross-pollinating wasps and developing fertile seeds inside ripe, sugary fruits eaten and dispersed by a host of tropical fauna. *Ficus* are pollen limited and it has been assumed that pollinated figs are inedible until after their wasps emerge. We observed leaf-cutter ants (*Atta cephalotes*) carrying fallen *F. colubrinae* figs into their nests. These figs were not fully developed, and contained developing wasps, yet were prematurely ripened. We tested the hypothesis that premature ripening of pollinated figs by *F. colubrinae* is an adaptive strategy for ensuring dispersal of its seeds by ants. If adaptive, premature ripening should be triggered actively by tree physiology rather than by exposure to light or heat. Also, mature figs should be more attractive to foraging ants than immature figs that have not yet developed seeds. On experimental branches held in different light environments in the lab, premature ripening was more common in the high light treatment than under ambient conditions. Ants showed a strong preference for prematurely ripened figs over unripe and mature figs, but took almost all figs over the course of 20 h. We conclude that a certain amount of premature ripening and subsequent fig loss is inevitable for trees in sun-exposed environments and is not evidence for adaptation to seed dispersal by ants. Furthermore, ant foraging behavior does not indicate that mature figs contain specialized attractants. That ants can and will take any fig on the ground does support the hypothesis that the seeds of *F. colubrinae* may be an ant-dispersed tree.

Key Words:leaf-cutter ants, seed dispersal,strangler figs

Introduction

Species in the genus *Ficus* are pollinated by obligate mutualist agaonid wasps (Janzen 1979). The adult female ("foundress") wasp enters a developing inflorescence ("syconium" or "fig") and pollinates its flowers in the process of ovipositing. The seeds and the wasp larvae inside them develop for ~ 3 weeks while the inflorescence begins to mature and ripen. Male and female wasp offspring mate before the fig becomes fully ripe and females emerge to repeat the cycle. Subsequent to wasp emergence, the fig becomes deep red, soft, and sugary, while nearly doubling in size. While this tight mutualism ensures the species-specific delivery of an individual's pollen, it has also resulted in pollen limitation of fig tree reproduction (Bronstein 1988).

Ficus syconia are eaten by a tremendous diversity of animals, including bats, howler monkeys, and birds. We observed leaf-cutter ants (*Atta cephalotes*) carrying immature figs to their nests. To our knowledge, this is the first evidence of predation on immature figs by any animal (Janzen 1983). We saw ants foraging for figs both in the canopy of and on the ground beneath a strangler fig (*Ficus colubrinae*). Over a 10 min. period, one nest collected 20 figs, 70 percent of which were red, but not fully developed (i.e., still small and firm), and the remainder pink. Inspection of the figs taken from the ants showed that 90 percent of the red figs and 10 percent of the pink figs contained foundress wasps. Further exploration revealed similar activity at two other conspecific trees.

The premature ripening of pollinated figs by a pollen-limited species encourages several biological questions. Primarily, is there a specialized relationship between ants and the tree? The figs of *F. colubrinae* are small (< 1.5 cm) and we observed no organism except *A. cephalotes* and one other unidentified species of ant foraging on them. Does the tree ripen the immature figs to establish ant foraging trails beneath its canopy, perhaps gaining the benefit of seed dispersal when the rest

of the fig crop matures?

We investigated the possibility that fig trees ripen some pollinated figs prematurely to later benefit from seed dispersal. Ripened immature figs appeared to be most abundant at the ends of distal, exposed branches of trees. Ripening may be due to adaptive tree physiology or it may simply be the result of exposure to high temperature and light. We subjected samples of branches to two different light/heat environments to test whether ripening can be induced by exposure without physiological input from the tree.

Further evidence for specialized interaction may lie in the foraging preference of the ants. If ants are to benefit the tree through dispersal of its seeds, then mature figs should be more attractive to ants than immature ripened or unripened figs. Lack of preference or preference based upon handling rate (mature figs are twice as large as immature figs) would suggest that ants are opportunistic foragers and that mature figs contain no particularly attractive compounds.

Methods

This study was conducted from 16 to 17 February at La Selva Biological Station in the Altantic lowlands of Costa Rica. To test *A. colombica* fig preference, we placed mature, ripe immature, and unripe immature figs under two *F. colubrinae* trees with visible leaf-cutter ant trails: one with figs on the ground under it, and a tree under which no figs were visible and leaf-cutter ants were carrying leaves. Ten ~ 5 cm^2 plots adjacent to leaf-cutter trails were selected under each tree. At each plot 15 figs were placed: 5 unripe immature, 5 ripe immature, and 5 mature. The number of figs in each category at each plot was counted 1 h and 20 h after placement. We analyzed ant preference for fig types under the two trees with a two-way ANOVA.

To test whether *F. colubrinae* ripening rate increases with sun exposure, we compared fig-bearing branches placed under a simulated sun environment with those placed in an ambient lab. Ten branch segments containing eight unripe figs each were pruned from a *F. colubrinae* tree. Five of these branch segments were placed under two 40 Watt bulbs at a distance of 10 cm from the bulbs. The other five branch segments were placed in an ambient (light and temperature) lab. We measured temperature at the branches at each site with a Physitemp™ thermometer; the light-exposure treatment was 1.5° C greater than the ambient treatment. After 15 hours we counted the number of figs that had turned pink on each branch. We analyzed the effect of light and heat on ripening with a t-test.

Results

More fruits reddened under conditions of high light and heat than under ambient conditions (t-test, $t = 6.93$, $df = 8$, $P < 0.0001$; Fig. 1). Leaf-cutter ants took significantly more ripe immature figs in 1 h than unripe or mature figs (ANOVA, $F = 40$, $df = 2$, $P < 0.0001$), regardless of tree (interaction $F = 1.85$, $df = 2$, $P < 0.17$). Ants took significantly more figs overall at one tree than the other (ANOVA, $F = 7.36$, $df = 1$, $P < 0.009$; Fig. 2).

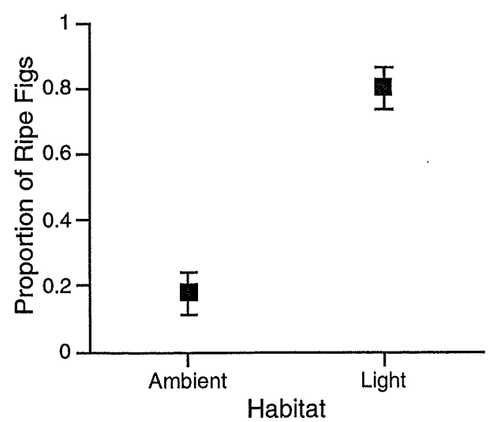

Fig. 1. Mean proportion of figs that ripened over 15 h in each of two controlled environments (± 1 SE). More figs ripened in the artificially lit and heated treatment than in the ambient treatment (n = 10).

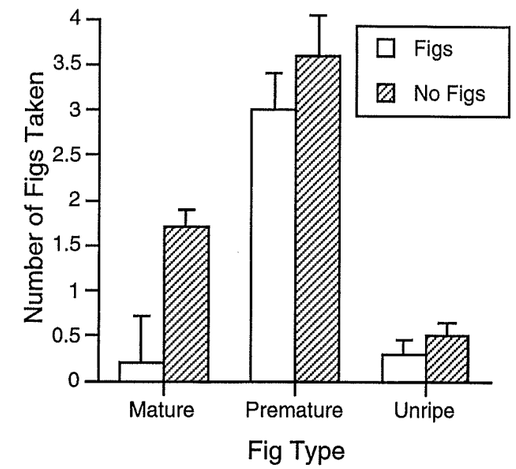

Fig. 2. Mean number of mature, ripe immature, and unripe figs taken (± 1 SE) from plots containing five of each fig type by *Atta cephalotes* in the first hour of a preference test under two *F. colubrinae* trees at La Selva Biological Station, Costa Rica (n = 60). One tree had naturally-fallen ripe immature and unripe figs on the ground underneath it, the other had no naturally-fallen figs at the time of the study.

Discussion

It appears most parsimonious that immature figs ripen due to exposure rather than as an adaptive strategy of the tree. *Ficus* trees do excise figs which are not pollinated (Janzen, 1979), and the possibility remains that premature ripening and excision is a means of reserving resources for less exposed (and more likely to fully develop) figs.

If *F. colubrinae* were specialized to seed dispersal by ants, we would expect its mature figs to be particularly attractive to ants. We found that ants prefer immature ripe figs to unripe and mature figs. Preference may be due to the smaller size and ease of handling of immature ripe figs. Ants responded quickly to the presence of our experimental figs and removed almost all figs of all types in 20 h, suggesting that figs are an important resource for the ants.

We did not find evidence of an adaptive advantage to premature fig ripening. However, our investigation was limited in its scope and leaves several important questions unanswered. We observed fig seeds scattered along ant trails leading from trees with mature figs, suggesting that ants could be effective short-range seed dispersers. Future studies could address the viability of figs in leaf-cutter ant nests, the presence of fig seeds in leaf-cutter ant waste piles, and the proportion of *F. colubrinae* trees associated with a leaf-cutter ant nest.

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