NOTES

The Acceptability of Young and Mature Leaves to Leaf-Cutter Ants Varies with Light Environment

The physical environment in which a plant is growing can have a strong influence on its susceptibility to herbivores (Coley et al. 1985). For example, light-induced differences in leaf traits can affect the selection of leaves by herbivores (Waterman et al. 1984; Harrison 1987; Ernest 1989; Nichols-Orians 1991a, b). In a previous study, I found that as light availability increases, the acceptability of mature leaves of Inga oerstediana, a tropical legume tree, to the leaf-cutter ant, Atta cephalotes, also increases (Nichols-Orians 1991a, b).

In addition to environmental conditions, leaf age may affect the selection of leaves by leaf-cutter ants (Cherrett 1972; Rockwood 1976, 1977; Waller 1982; Shepard 1985; Nichols-Orians & Schultz 1989, 1990). Leaf-cutters usually attack trees when young leaves are most available (Cherrett 1972), because young leaves are easier to cut and more nutrient-rich (Barrer & Cherrett 1972, Littledyke & Cherrett 1978, Waller 1982, Nichols-Orians & Schultz 1989). In studying the interactions between I. oerstediana and A. cephalotes (Nichols-Orians & Schultz 1990), it was found that young leaves, despite very high concentrations of nutrients, were less chemically acceptable than mature leaves; this was apparently due to a higher concentration of condensed tannin in the young leaves. A number of researchers have identified similar patterns in other plant/herbivore systems (Ikeda et al. 1977, Raupp & Denno 1983, Meyer & Montgomery 1987).

Mole & Waterman (1988) suggest that light availability can alter the relative acceptability of young and mature leaves, but few studies have assessed if and how environment mediates the acceptability of young and mature leaves to herbivores (Ernest 1989). Because the production of secondary chemicals (in this case condensed tannins) and nutrients is dependent upon light availability (Chandler & Goosm 1982, Mole et al. 1988, Denslow et al. 1990), the relative acceptability of young and mature leaves of I. oerstediana to leaf-cutter ants may be modified by light availability. Although young leaves of I. oerstediana plants in full sun are less acceptable to leaf-cutter ants than mature leaves from the same plant (unless Nichols-Orians & Schultz 1990), I hypothesized that for plants in the shaded understory, young leaves would be more acceptable than mature leaves. Shaded young leaves are thought to have a higher nutrient to tannin ratio than do shaded mature leaves (Mole & Waterman 1988).

In May of 1988 three colonies of Atta cephalotes (L.) were located at the La Selva Biological Station in the Atlantic lowlands of Costa Rica (10°26'N, 83°59'W). I used saplings of Inga oerstediana Benth. (Fabaceae: Mimosoideae), formerly Inga edulis var. minutula Schery (Nichols-Orians & Schultz 1990), because the saplings can be found growing in different light environments and because they are naturally attacked by leaf-cutter ants (C. Nichols-Orians, pers. obs.). Six saplings were located growing in the understory and six growing in large gaps. Saplings were 0.5 to 1.0 m in height. I employed a paired design, collecting both mature and young leaves from the same plant. Mature leaves were defined as those that were fully expanded and dark green, but devoid of epiphylls because epiphylls affect the acceptability of leaves of leaf-cutter ants (Mueller & Wolf-Mueller 1991). Young leaves were those that were close to fully expanded and still slightly red in color.

The leaves were transported to the study colonies and used in a behavioral assay to determine how the light environment of a plant influences the selection of young and mature leaves by foraging ants. Two types of assays are often employed to evaluate the susceptibility of plants to leaf-cutter ants. The "pickup" assay is designed to determine preferences based on chemical differences, defensive or nutritional, between leaf types (Howard 1987). In this assay precut leaf discs are presented to the ants and removal of the discs monitored. Conceivably water content, physical features of a leaf (e.g., trichomes), or leaf mass could influence disc removal. Water content does not appear to affect disc removal in this system (C. Nichols-Orians, pers. obs.). Also, I have not identified any physical features in I. oerstediana which could interefere with removal. Finally, leaf mass appears unimportant. The leaf discs were small enough that all foraging ants could easily pick up these leaf discs. In fact, the toughest and heaviest leaf type assayed to date was one of the most acceptable leaf types (Nichols-Orians & Schultz 1990).

The second assay, the "cutting" assay, is used to determine if physical features interfere with the cutting of leaves already selected by the leaf-cutter ants (Howard 1988; Nichols-Orians & Schultz 1989,
1990). I did not employ the "cutting" assay because I was only interested in determining how leaf age and environment influence the initial selection of leaves.

In the "pickup" assay, two leaf discs (produced with a standard paper punch) of each leaf type were placed along the trail. To ensure that the assays involving the leaf types were independent, I separated them spatially along the trail and randomized the order of presentation each day. When one disc was removed it was replaced by a like disc. The chemical acceptability of a given leaf type was expressed as the percentage of the total number of leaf discs removed in 30 min. The assay was repeated twice and the replicates averaged to give a single acceptability value for each leaf type. The assays were repeated six times on colony 1, three times on colony 2, and twice on colony 3. Because *I. oerstediana* leaves are compound, I only used leaf discs from distal leaflets in the assay, in order to avoid possible leaflet position effects (Gall 1987).

A nonparametric sign test, SYSTAT statistical package, was employed to determine if there were differences among leaf types in acceptability. A nonparametric test was used because the data were not normally distributed.

Bioassays with the ants indicate that all colonies showed the same preferences for the four different leaf types (Colony Effects \(P > 0.10\)). This result is consistent with previous work that showed that even though leaf-cutter ants may differ in their willingness to accept leaves of *I. oerstediana* (Nichols-Orians & Schultz 1990), they still show the same relative preferences for different leaf types (Nichols-Orians & Schultz 1990, Nichols-Orians 1991a). Because there were no colony effects, the data were analyzed without colony as an effect.

Consistent with previous work, the ants preferred leaf discs from plants growing in high light over leaf discs of plants growing in the shaded understory \((P \leq 0.01)\), and leaf discs of mature sun leaves over those of young sun leaves (Fig. 1) (Nichols-Orians 1991a, b). However, no differences were found in the acceptability of young and mature leaves of understory plants (Fig. 1). This result is contrary to my original hypothesis. I had hypothesized that young shade leaves would be more acceptable to the ants than mature shade leaves, because young leaves would have a higher nutrient to tannin ratio (*sensu* Mole & Waterman 1988). I was unable to collect sufficient leaf material to do chemical analyses as well as behavioral assays, and therefore cannot provide a possible mechanism for the differential acceptability. Nevertheless, the data indicate that the relative acceptability of young and mature leaves can be modified by light availability.
The survival of some herbivores appears to depend upon the presence of young leaves (Aide & Londoño 1989). In these cases young leaves might be expected to be preferred under all light environments. Perhaps for herbivores like leaf-cutter ants, that attack both young and mature leaves, the relative acceptability of young and mature leaves will be modified by light availability. Other environmental conditions, such as soil quality, can affect leaf traits (e.g., Denslow et al. 1990) and acceptability (Nichols-Orians 1991b), and may influence the relative acceptability of leaves of different ages as well. Clearly, for some herbivores, generalizations on the acceptability of young and mature leaves may require that studies be conducted under different environmental conditions.

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Fig Dimorphism in Bird-Dispersed Gynodioecious Ficus

In Malaysian lowland rain forests, at least 29 species of Ficus have bird-dispersed figs (Lambert 1989). Eight of these species belong to the subgenus Ficus, and are gynodioecious. Plants of these gynodioecious species produce either gall figs or seed figs. Gall figs contain both male and female florets, but effectively become males because the female florets have relatively short styles and are predated by the larvae of agaonid wasps, which are the species-specific pollinators of Ficus. In contrast, the styles of seed figs are longer, so that incoming agaonids pollinate the florets but cannot oviposit eggs in them. Seed figs therefore produce seeds, but are not a source of pollen-carrying agaonids (Janzen 1980, Verkerke 1989).

Hill (1967), working mainly in Hong Kong, stated that there were no external morphological differences between gall and female plants except for differences in the shape and size of the figs, and sometimes in their color and seasonal occurrence. In southeast Asia, these differences have not been previously documented.

A comparison of the figs from three gynodioecious bird-dispersed strangling Ficus species [F. heteropleura Bl., F. obscura Bl. (var. borneensis Miq.) Corner, and F. parietalis Bl.] at Kuala Lompat, West Malaysia (3°43'N, 102°17'E, 50–80 m altitude) showed that there were distinctive, consistent differences in color, texture, and morphology between figs on male and female plants.

Gall figs were always paler in coloration than their respective seed figs, and did not exhibit the striking color changes associated with the ripening of the latter. Thus the gall figs of F. obscura were whitish, becoming blotchy brown before dropping, in contrast to the bright orange seed figs which ripened dark red to purple. The gall figs of F. heteropleura and F. parietalis were pale orange at all stages, while both species produced orange seed figs which ripened dark red. The texture of gall figs was rubbery at the stage before falling, but never developed the characteristic soft, fleshy nature of bird-dispersed seed figs. Ostioles of the gall figs of F. parietalis were notably large and appeared to open just before the gall figs fell to the ground. The broad, open ostioles of F. parietalis presumably assist the escape of pollen-laden female agaonid wasps. In contrast, seed figs of F. parietalis did not have distinctive, open ostioles at any stage of ripeness.