8 Epiphytic Associations with Ants

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8.1 Ubiquity and Sociality of Ants: Diversity of Ant-Epiphyte Relations

Ants are the most common arboreal insects of tropical forests (Leston 1973; Erwin 1983; Wilson 1987) and possibly the most frequent animal contacts of epiphytic plants. It is not surprising, then, that epiphytes share a number of ecological interactions with ants, and that some of these interactions have become prominent features of epiphyte biology. Not only are ants abundant and ubiquitous, but their unique social attributes proffer a functional significance disproportionate to numbers. As eusocial insects (Wilson 1971), ants exhibit a division of colony labors between reproductive and sterile (worker) castes. Primary responsibility for more dangerous, extranidal activity resides with the workers, and the colony as a reproductive unit often enjoys considerable immunity from predation (Wilson 1971; Jeanne and Davidson 1984). Consequently, ant populations are often limited by food and/or nest sites (e.g. Wilson 1959; Leston 1973; Swain 1977; Brown and Davidson 1977) and are likely to be responsive over both ecological and evolutionary time to the provisioning of such resources by epiphytes and other plants. Relatively long life expectancies allow many ants to divert considerable energy and resources early in the life history to modifications of the nesting and foraging environments (Forel 1929). In turn, these modifications may further counteract negative abiotic and biotic selection pressures and further prolong colony lifespans. Thus, for epiphytes forming associations with ants, these associations can often be sustained over a biologically significant fraction of the life histories of even slow-growing species.

A great deal of diversity is represented in ant-epiphyte interactions. Part of this diversity is phenomenological. For example, while some epiphytes are colonized by ant colonies or alate reproductives, others colonize ant nests via highly directional dispersal of seed propagules. In constancy and species specificity, ant-epiphyte interactions range from the occasional, opportunistic and polyphilic to those that are monophilic and possibly obligate and coevolved. All along this spectrum, there are differences in the effects that epiphytes have on ants and vice versa. Finally, some ant-epiphyte associations are locally

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common and likely to play prominent roles in ecosystems, whereas others are rare, and their effects on other organisms weak or obscure. The goal of this chapter is to review the range of ant-epiphyte interactions in an attempt to relate phenomenology, obligacy and specificity, and abundance and significance in ecosystems. We begin with opportunistic ant-epiphyte interactions, which suggest plausible origins of myrmecophytic epiphytes.

8.2 Opportunistic Associations of Epiphytes and Ants

8.2.1 Carton as Epiphyte Substrate

Most occasional relationships between ants and epiphytes are based on what Longino (1986) has recently argued is the widespread use of ant carton as epiphyte substrate. Many tropical ant species, in such successful genera as *Azteca*, *Hypoclinea* and *Iridomyrmex* (Dolichoderinae), *Crematogaster* and *Pheidole* (Myrmicinae) and *Camponotus* and *Polyrhachis* (Formicinae), construct nests from a variety of materials ranging from plant fibers and thin bark to decaying leaves, sand, soil and organic debris (Wheeler 1910; Forel 1929). These nests take a variety of forms (Fig. 8.1a-d). Some, flattened against tree trunks or appended beneath major branches have thin and sturdy but nutrient-poor, parchment-like walls inappropriate for plant growth. More important for epiphytes are cartons formed from loose accumulations of earthen material or organic debris with ant galleries ramifying internally (see Table 8.2). Such amorphous carton masses may be lodged in tree crotches and crevices, under and around loose bark and in hollow stems or other plant cavities. Carton materials are thought to be cemented with secretions of ant maxillary and mandibular glands (Wheeler 1910; Forel 1929), but presently little is known of the potential effects of ant secretions on plant growth. Fungi live symbiotically in some ant cartons (Forel 1929; Maschwitz and Hölldobler 1970), and their absence from other cartons is presumably due to fungistatic secretions of ants (Kerr 1912). Fungistats are produced by the metapleural glands (Maschwitz 1974; Maschwitz et al. 1970) or mandibular glands (*Camponotus*, Blum et al. 1988) of most ants (Hölldobler and Engel-Siegel 1984). These compounds appear to suppress nest pathogens and may also affect growth of mycorrhizae. As metapleural products are known to include plant growth hormones IAA and PAA (Maschwitz et al. 1970; Schildknecht and Koob 1970, 1971), the secretions may even directly affect growth of the epiphytes themselves.

Associations of epiphytes with potentially nutritive ant carton may arise by one or more of at least three nonexclusive mechanisms, whose relative importance is difficult to assess from present data. First, founding queens or established ant colonies may colonize epiphytes whose protective foliage or accumulated organic debris excludes potential predators and/or furnishes a ready source of materials for nest construction. This behavior is particularly characteristic of phylogenetically older ant lineages such as ponerines *Pachy-