

Ant – Plant Interactions

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Symbiosis of ants with *Cecropia* as a function of light regime

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Introduction

The relationships between ants and myrmecophytes are still viewed by many as unique and curious phenomena, unrelated to mainstream evolutionary ecology. However, as argued by McKey (1988), renewed interest in these relationships is leading to the discovery of both pattern and complexity resembling that found in other ecological systems. First, certain unifying principles of plant defence theory may be generalized to ant-protection mutualisms (McKey 1984, 1988). In addition, symbiotic ant-plant relationships are likely to be products of selection based on complex networks of direct and indirect interactions, the outcome of which can be modified by variation in the physical environment (e.g. Schemske and Horvitz 1988; Davidson and Epstein 1989; Davidson *et al.* 1990). Given these parallels with other ecological systems, symbiotic ant-plant associations may have a unique role to play in elucidating the determinants of evolutionary specialization. Both myrmecophytes and plant-ants vary in their degree of specialization, and this variation can be quantified explicitly by experiment, and related to present-day selection environments.

To characterize factors driving evolutionary specialization in these relationships, it is necessary to describe the environmental context in which the associations evolve. The framework developed here draws principally on studies of myrmecophytic *Cecropia* in western Amazonia (Davidson *et al.* 1990). However, some of the patterns noted may apply both to Central American *Cecropia* (Longino 1989a, Chapter 19, this volume) and to other ant-plant symbioses (Davidson *et al.* 1990).

Myrmecophytic *Cecropia* and their ants

Cecropia (Cecropiaceae) is the most widespread and important genus of early successional trees in neotropical forests, and most of the more than 100 species host symbiotic ants (C. C. Berg, personal communication). All myrmecophytic *Cecropia* provide similar benefits to ants. Early in sapling growth, hollow stems expand and internodes develop with prostomata, or

small areas of unvascularized tissue, where queens enter stems without rupturing phloem and flooding internodes with mucilage. Colonies develop within these stems, and emerging workers collect glycogen-rich Müllerian bodies at the bases of petioles on hairy platforms termed trichilia (Rickson 1971, 1973, 1976). The production of pearl bodies on lower leaf surfaces is variable among *Cecropia* species.

Although early naturalists noted a diversity of ant genera dwelling in *Cecropia* stems (e.g. Wheeler 1942), recent ecological studies have emphasized associations with *Azteca* ants (Dolichoderinae). *Azteca* species predominate on fast-growing *Cecropia* in open, sunny environments. Trees growing slowly in shaded habitats are often occupied by specialized *Cecropia* ants in other genera, including *Pachycondyla* (Ponerinae), *Camponotus* (Formicinae), and *Crematogaster* (Myrmicinae) (Davidson *et al.* 1989; 1990; D. W. Davidson and B. L. Fisher, unpublished work). *Cecropia* seedlings receive significant protection from at least some ant associates which repel insect herbivores (Schupp 1986) and/or remove encircling vines (Janzen 1969; Davidson *et al.* 1988).

***Cecropia* in south-eastern Peru**

Our studies have focused on the *Cecropia* of tropical moist forests of south-eastern (Madre de Dios) Peru (Davidson *et al.* (in press)). Three pairs of closely related species appear to be included among six *Cecropia* species which are common at Reserva Tambopata and the Estación Biológica de Cocha Cashu (including borders of the Rio Manu from Cocha Cashu to Tayacome). *Cecropia membranacea* and *Cecropia tessmannii* (a name used in ornithological literature (Koepcke 1972) but not yet confirmed) are difficult to distinguish by vegetative morphology. Once classified as subspecies, they differ conspicuously only in developmental and myrmecophytic traits (see below), but are quite distinct from other species. *Cecropia engleriana* and *Cecropia* sp. A differ strikingly from one another as seedlings and early saplings but are difficult to distinguish by vegetative characters later in development. Seeds from individual maternal parents of both species occasionally give rise to seedlings that are morphological intermediates. Either the two species may hybridize, or their separate gene pools may not yet have eliminated particular gene combinations that lead to similar morphology. The last two species, *Cecropia polystachya* and *Cecropia ficifolia* also bear a striking resemblance to one another in vegetative phenotypes, but are very distinct from the other species pairs. Since the characteristic habitats of each of the six *Cecropia* species differ markedly from those of postulated close relatives, morphological similarities within pairs are unlikely to reflect evolutionary convergence. Both the Peruvian *Cecropia* and their symbiotic ants exhibit strong habitat specificity, and the distributions of at least some ant associates are related more obviously to habitat than to host species (David-

son *et al.* 1990). Apparently a very general feature of the symbiosis, the habitat specificity of both *Cecropia* and its specialized ants occur principally with respect to difference in the light regime (Benson 1985; Harada and Benson 1988; Longino 1989a). To explain the pattern, we consider how light intensity may affect the allocation of plant resources to growth and defence and, consequently, the resources available to ants.

Patterns of plant investment in defence

In all ecological systems, variation in the physical environment sets the pattern of resource availability at successive trophic levels. Ecological and evolutionary responses of myrmecophytes to variation in their own resource environments should then determine rates of resource supply to ants in symbiotic ant-protection mutualisms. Plant responses can be investigated at two levels. First, environmental variation often correlates predictably with proportionate investment in growth versus defence. Secondly, for any given level of defence, relative allocation to biotic versus chemical (or physical) defences may also exhibit a pattern in relation to the environment.

Total defence investment

Circumstantial evidence suggests that both biotic and chemical defence of myrmecophytic *Cecropia* may be costly, and may compromise the capacity for rapid growth. First, *Cecropia* populations growing without their specialized ants tend to lose the ability to produce trichilia (Janzen 1973; Rickson 1977; Putz and Holbrook 1988). Secondly, intraspecific variation in leaf tannin levels is negatively correlated with rates of leaf production in Central American *Cecropia peltata* L. (Coley 1986). Thirdly, interspecific differences in the defence investment of myrmecophytic *Cecropia* in western Amazonia are correlated with habitat in a manner predicted from tradeoffs between growth and defence (Davidson *et al.* 1990). In south-eastern Peru, *C. membranacea*, *C. engleriana*, and *C. polystachya* grow regularly at high light intensities in large disturbances along major watercourses, and in clearings associated with human habitation (Table 20. 1). Here, competition from fast-growing pioneer species of similar size places a premium on rapid growth, and the smallest *Cecropia* in these habitats usually die before reproducing (J. Terborgh, unpublished work).

The apparent closest relatives of light-demanding species establish mainly within small forest light gaps, in the shade of much larger and older neighbours. For these species, diversion of limiting carbon from defence to growth might confer little advantage but jeopardize the persistence required to take advantage of later canopy openings. Not surprisingly, shade-tolerant gap species develop their trichilia at earlier leaf nodes (Fig. 20. 1) and at smaller sizes than do closely related congeners of more open environments. Moreover, in the three pairwise comparisons, preliminary data indicate greater dry

Table 20.1. Percentage contributions of six species to total *Cecropia* across habitats in south-eastern Peru. Values for relatively large plants and small seedlings (in parentheses)*.

<i>Cecropia</i>	% Contribution of species to <i>Cecropia</i> in habitats			
	Forest gaps	Human clearings	Stream banks	River banks
Light-demanding species				
1. <i>membranacea</i> Trec.	0 (3)	0 (19)	98 (62)	85 (66)
2. <i>engleriana</i> Sneathlage	0 (0)	48 (39)	0 (8)	0 (3)
3. <i>polystachya</i> Trec.	1 (2)	52 (32)	2 (28)	15 (28)
Shade-tolerant species				
1. <i>tessmannii</i> Mildbr.	36 (36)	0 (5)	0 (0)	0 (3)
2. species A	31 (34)	0 (5)	0 (2)	0 (0)
3. <i>ficifolia</i> Warb.	32 (25)	0 (0)	0 (0)	0 (0)
Sample size	94 (67)	21 (57)	45 (50)	13 = 173 (67) (241)

* *Cecropia engleriana* also occurs frequently along streams and rivers but was uncommon where we worked. Like-numbered light-demanding and shade-tolerant species are thought to be close relatives.

weight production of Müllerian bodies in shade-tolerant species (Table 20. 2). These same species tend to have a greater percentage of trichilia active at a given time (Table 20. 2, two of three comparisons only, see below). If alternative chemical defences were strongly reduced with the acquisition of biotic defence (P. D. Coley, personal communication for *C. peltata*), then shade-tolerant species would have proportionately greater total defence investment than their light-dependent counterparts after the onset of myrmecophytism. Both the slower intrinsic growth rates of shade-tolerant species (Fig. 20. 2) and a delay in trichilia development at low light intensities (intraspecific comparisons, Fig. 20. 3) also support the hypothesis that these carbon-based defences are costly.

Patterns in the biotic defence of *Cecropia* are remarkably similar to those exhibited by chemically defended plants under different light regimes

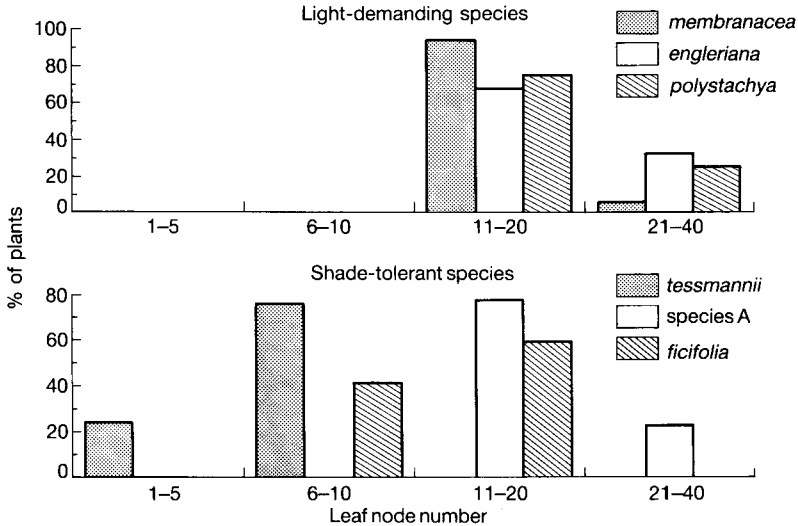


Fig. 20.1. Distributions of leaf node numbers for the first leaf with trichilia, for six Peruvian species of *Cecropia* grown in tropical greenhouses in Utah. Relationships for closely related species pairs were: *C. tessmannii* < *C. membranacea* ($P < 0.00001$); *Cecropia* sp. A. < *C. engleriana* ($P = 0.06$), and *C. ficifolia* < *C. polystachya* ($P < 0.00001$). Mann-Whitney U-Tests were two-tailed.

(Janzen 1974b; Bryant *et al.* 1983; Coley *et al.* 1985). In intraspecific comparisons of carbon-based chemical defences, secondary compounds occur at higher concentrations in environments of high light intensity (e.g. Woodhead 1981; Waterman *et al.* 1984; Larsson *et al.* 1986; Müller *et al.* 1987; Mole *et al.* 1988), or where plants are limited by nutrients other than carbon (e.g. nitrogen, Bryant *et al.* 1985). This trend is commonly reversed in interspecific comparisons, probably because greater defence investment is an adaptation to slower growth rates and longer leaf lifetimes (Coley 1983; Coley *et al.* 1985; Bryant *et al.* 1985; Bazzaz *et al.* 1987; Coley and Aide 1990). However, the pattern may vary with plant growth form. Some understorey shrubs grow at low light levels throughout their lives and exhibit lower defence investment at reduced light in interspecific comparisons (see Baldwin and Schultz (1988) for Melastomataceae). It is not yet possible to compare total defence investment by myrmecophytes across such disparate lifeforms.

Investment in biotic versus chemical defence

If defence is costly, plants should avoid investing in redundant defence systems, but deploy alternative systems in ways contingent on their relative

Table 20.2. Production of Müllerian bodies by trichilia in three pairs of Peruvian *Cecropia* species. Plants were grown in a temperate greenhouse, but were not standardized for history or size.

<i>Cecropia</i> species ^a	Mass of MBs ^b (mg d ⁻¹)	% Active trichilia ^c
<i>tessmannii</i> (ST)	7.3	50
	6.7	57
<i>membranacea</i> (LD)	5.3	86
	4.3	76
	—	64
species A (ST) ^d	7.2	82
	10.1	89
<i>engleriana</i> (LD)	1.2	69
	2.7	60
<i>ficifolia</i> (ST)	24.4	92
<i>polystachya</i> (LD)	2.2	67
	1.6	56

^a ST = shade tolerant and LD = light-demanding member of species pair.

^b 24-hour production of Müllerian bodies (MBs) by trichilia of the two youngest leaves. Food bodies are produced in irregular pulses, but production peaks at dusk in all species. Irregularity may stimulate relatively constant attention by ants.

^c Percentage of trichilia actively producing Müllerian bodies on plants whose leaves all have trichilia. Production declines regularly with leaf age.

^d Leaf size of *Cecropia* species A is approximately one-third that of other species; production of Müllerian bodies, per unit leaf area, is greatest in this species.

cost effectiveness in different circumstances. Chemical defences have been reduced or lost in some myrmecophytes (Janzen 1966; Rehr *et al.* 1973; Siegler and Ebinger 1987; Jolivet Chapter 26, this volume), but other ant-plants are protected by secondary compounds early in development, when ant defence is lacking or unreliable. Young seedlings with few total resources may grow too slowly or unevenly to maintain ant colonies. Not surprisingly, many ant-plants delay expression of myrmecophytic traits until later in seedling or sapling development (Janzen 1975; Davidson *et al.* 1990; D. W. Davidson, personal observation). Like *Barteria fistulosa* (Passifloraceae) (Waterman *et al.* 1984), myrmecophytic *Cecropia* apparently have chemical protection in their leaves prior to producing ant-attractive traits (Coley 1986; P. D. Coley, personal communication for *C. peltata*). Each of the six Peruvian *Cecropia* species has measurable leaf concentrations of condensed tannins, although we do not yet have data on hydrolyzable tannins, nor on developmental and interspecific trends in total tannins.

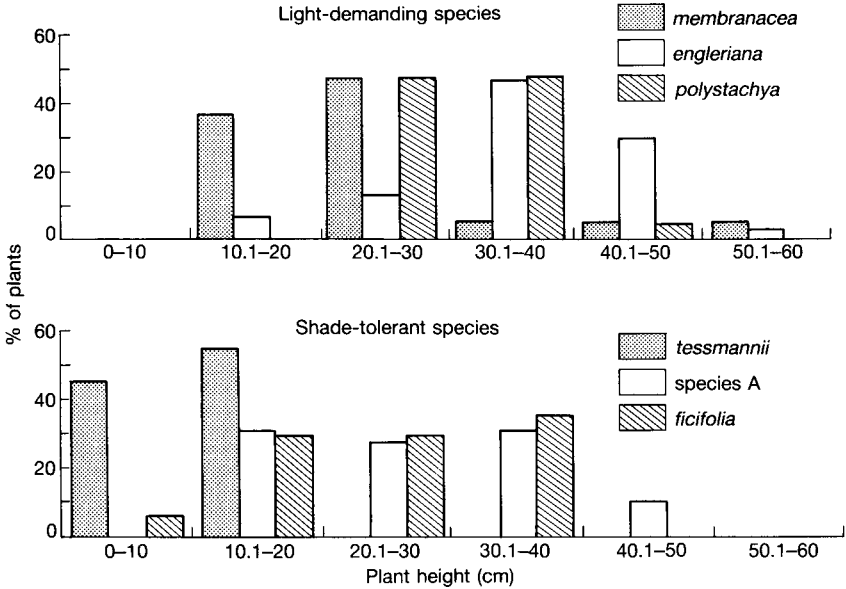


Fig. 20.2. Distribution of plant sizes for six Peruvian *Cecropia* species after eight months of cultivation from seed in the University of Utah tropical greenhouse (July 1987–February 1988). The exception, *C. tessmannii*, was grown from January 1987–October 1987, and its growth was related to that of the other species indirectly, by comparisons with *C. engleriana* cultivated independently during both growth trials. Larger individuals of *C. membranacea* are probably more representative of the species' potential for rapid growth. A significant fraction of its seedlings were stunted at the outset for unexplained reasons. Growth rates of related species differed significantly in two-tailed Mann–Whitney U-Tests: *C. membranacea* > *C. tessmannii* ($P < 0.0001$); *C. engleriana* > *Cecropia* sp. A. ($P \approx 0.002$), and *C. polystachya* > *C. ficifolia* ($P < 0.05$). Sample sizes ranged from 17 to 30.

Weighing the disparities in the synthesis and maintenance costs of biotic and chemical defences, McKey (1984, 1988) concluded that habitat-correlated variation in plant growth patterns should determine relative investment in the two defence systems. Food and domatia for ants must be synthesized continuously and should have higher maintenance costs than chemical defences like tannins and lignins. However, the non-toxic constituents of food rewards may be reclaimable and more easily shunted from senescent leaves to new growth. Ant defences then take the place of phenological defences in plants with continuous leaf production and rapid leaf turnover. In contrast, because chemical defences such as tannins and lignins have relatively high synthesis costs but low maintenance costs, their net benefit should increase with the lifespan of the plant part. These

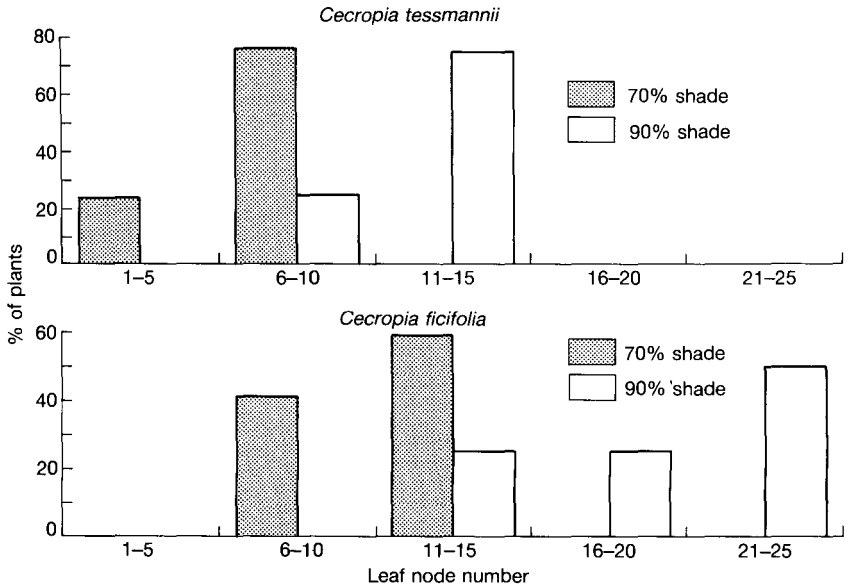


Fig. 20.3. Distributions of leaf node numbers for the first leaf with trichilia in two shade-tolerant *Cecropia* species grown in the University of Utah tropical greenhouse. A 70 per cent shade cloth covered the greenhouse bays to shield tropical plants from intense sunlight. Additional shading significantly delayed trichilia development in both species (in two-tailed Mann-Whitney-*U*-Tests, $P = 0.002$ (*C. tessmannii*) and $P = 0.003$ (*C. ficifolia*). Conceivably, selection for the timing of trichilia development could be uniform across shade-tolerant and light-demanding species, with shade-tolerant saplings showing earlier onset of myrmecophytism only at comparatively high light levels in the greenhouse (comparing Fig. 20.1 with Fig. 20.3). However, two factors suggest the interpretation that selection has favoured earlier myrmecophytism in shade-tolerant hosts. First, the growth form of greenhouse seedlings at 70 per cent shade is entirely normal, while that of 90 per cent shaded plants is unusually elongate with narrow internodes. This suggests that field seedlings grow at light levels higher than 90 per cent shade. Nevertheless, even comparing shade-tolerant species grown at low light with light-demanding species grown at high light, shade-tolerant and light-demanding species differ in the same direction as in the comparisons in Fig. 20.1.

non-reclaimable chemical defences are more typical of plants with long-lived leaves. Even specialized ant-plants with continuous leaf production may protect mature leaves chemically, if long leaf lifetimes make the continuing costs of ant defence uneconomic (McKey (1984) for *Leonardoxa africana*).

Leaf lifetimes and tannin concentrations must be measured under natural conditions in the field, and we do not yet have such data. However, in many non-myrmecophytes, leaf lifetimes vary inversely with intrinsic growth rate (e.g. Chabot and Hicks 1982; Mooney and Gulmon 1982). If the extremely

slow growth rate of *C. tessmannii* (Fig. 20. 2) is indicative of especially long leaf lifetimes, mature leaves would be defended more economically by tannins than by ants. Mature leaves of greenhouse *C. tessmannii* have moderate to high concentrations of condensed tannins. Interestingly, this species had the lowest percentage of leaves with active trichilia, despite the relatively high percentages of ant-defended leaves in the other two shade-tolerant species (Table 20. 2). This species is also unique in lacking pearl bodies on leaf under-surfaces. In contrast, *Cecropia* sp. A, the species with the greatest investment in biotic defences per unit leaf area (Table 20. 2), had the lowest levels of condensed tannins (proanthocyanin assay in greenhouse saplings with trichilia) measured for mature leaves of any of the six species. Comparatively high tannin concentrations might characterize *Cecropia* species that often house parasitic ants, i.e. ants that are relatively poor host plant defenders (Janzen 1975; McKey 1984; Davidson *et al.* 1990). *Cecropia ficifolia* may have the highest frequency of occupation by parasitic ants (*Camponotus balzani*, Table 20. 3, but see below), and levels of condensed tannins were highest in leaves of this species.

Rates of resource supply to established ant colonies

Rates of resource supply to young ant colonies depend not just on the host plant's proportionate investment in biotic defence, but on plant size and rate of leaf production at colonization. Somewhat counter-intuitively, then, light-demanding *Cecropia* may represent better resources than shade-tolerant species at the stage when ant workers first emerge on the plant surface. Rates of resource provisioning should be greater in light-demanding species because of a combination of factors:

1. higher light intensities that promote rapid growth in the characteristic habitats;
2. faster intrinsic growth rates (positively correlated with new leaf production); and
3. larger sizes at colonization, together with size-dependency in growth rates.

Rates of Müllerian body production decline with leaf age in all the Peruvian *Cecropia* and, on average, active trichilia may be newer and more productive on fast-growing, light-demanding species.

Figure 20. 4(a) and (b) summarizes the hypothesized relationship between leaf lifetimes (presumed negatively correlated with intrinsic growth rate), defence investment, and rate of resource provisioning to ants. These hypotheses are preliminary because none of our measurements of resource supply were made under natural conditions, where light-demanding and shade-tolerant species grow in very different resource environments (including

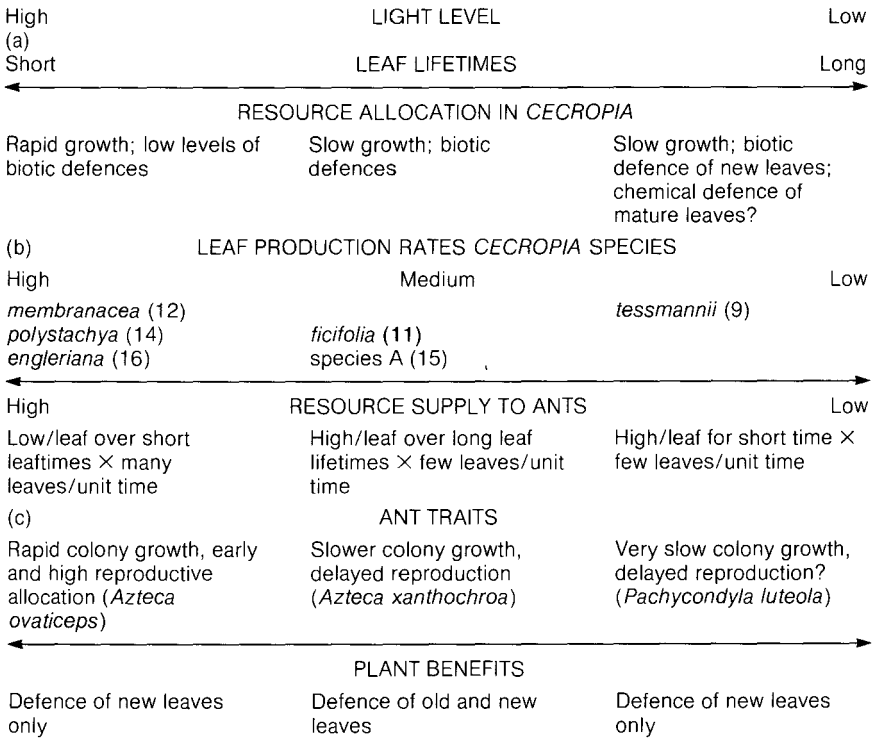


Fig. 20.4. (a) Hypothesized relative investment by *Cecropia* in growth versus defence, in relation to average leaf lifespan (assumed proportional to growth rates). (b) Hypothesized relationship between leaf production rates of particular *Cecropia* species and rates of resource supply to ants. In parentheses are numbers of leaves and leaf scars at the end of the greenhouse growth experiment; the numbers are equated with leaf production rates. In the field, leaf production rates should be proportionately much greater for light-demanding species (left-hand column) than for related shade-tolerant species (centre and right-hand columns), because of far greater light intensities in the typical habitat. (c) Ant traits and plant benefits correlated with patterns of resource provisioning to ants in (b).

red/far red light ratios which are known to affect plant development, Lee 1986).

Specialized ants of *Cecropia*

Early tropical naturalists recorded, without interpretation, much variability in the species composition of ant-plant associations (e.g. Bequaert 1922; Wheeler 1942; summarized in Huxley 1986). Relationships of most myrmecophytes and plant-ants are oligophilic, with taxonomic or functional ant-

plant guilds, regularly associated with small guilds of specialized congeneric or unrelated ants. Four ants of *Cecropia* in south-eastern Peru (Table 20. 3) can be classified as specialists because:

1. they occur on no other myrmecophyte genus;
2. queens colonize hosts principally at prostomata;
3. they recognize Müllerian bodies as food; and
4. except for *Camponotus balzani*, they reject standard ant baits like tuna and cheese.

Competition between specialized ants

Many ant-plants have a modular structure which allows colonization of leaf or stem domatia by several foundresses of one or more species. Multiple colonization should lead to intense intra- and interspecific competition among incipient colonies for dominance of the host plant. Competition for hosts is usually resolved with the emergence of the first young colony, whose

Table 20.3. Percentages of four specialized *Cecropia* ants on six *Cecropia* spp. from south-eastern Peru. Values for larger plants with established colonies and for seedlings with only foundresses or incipient colonies (in parentheses).

<i>Cecropia</i>	<i>n</i> *	<i>Azteca</i> <i>ovateiceps</i>	<i>Azteca</i> <i>xanthochroa</i>	<i>Camponotus</i> <i>balzani</i>	<i>Pachycondyla</i> <i>luteola</i>
Light-demanding species					
1. <i>membranacea</i>	53	49	21	30	0
	91	(48)	(18)	(15)	(20)
2. <i>engleriana</i>	6	83	17	0	0
	41	(10)	(76)	(15)	(0)
3. <i>polystachya</i>	7	57	29	14	0
	64	(12)	(77)	(11)	(0)
Shade-tolerant species					
1. <i>tessmannii</i>	31	0	0	10	90
	49	(0)	(2)	(12)	(86)
2. species A	17	0	100	0	0
	43	(0)	(100)	(0)	(0)
3. <i>ficifolia</i>	24	0	48	52	0
	18	(0)	(83)	(17)	(0)

**n* = Total number of trees sampled per *Cecropia* species (or, for seedlings, total number of foundresses or incipient colonies censused per *Cecropia* species). Data from combined censuses at Reserva Tambopata and Estación Biológica de Cocha Cashu, Peru.

workers kill all remaining colonies. Thus, Davidson *et al.* (1989) demonstrated negative associations between alternative ant taxa for populations of six myrmecophytes (in six genera) tested after worker emergence, but none of four hosts tested before colonies were active on plant surfaces. *Cecropia tessmannii* with established colonies housed either *Pachycondyla luteola* or *Camponotus balzani* but not both. Similar negative associations among ants are evident from Longino's (1989) data on Central American *Cecropia*.

Included niches in relation to a variable physical environment

The species of ants associated with particular *Cecropia* species often change abruptly across habitat boundaries, within as well as between host plant species (Benson 1985; Longino 1989; Davidson *et al.* 1990). This pattern suggests that the relative success of different ant species could differ in response to rates of resource supply, governed by resource availability to hosts (Davidson *et al.* 1990). For example, in south-eastern Peru several *Cecropia* species can house established colonies of either *Azteca ovaticeps* (see Chapter 19), *Azteca xanthochroa*, or *Camponotus balzani* (Table 20. 3). While the former species predominates in the most favourable plant resource environments along banks of major rivers (high light and alluvial soils), the latter two species dominate numerically at reduced light intensity inside the forest edge, or on poorer soils along steep banks of minor streams, and in large clearings on high terraces. Together with *A. ovaticeps*' apparent restriction to relatively fast-growing *Cecropia* species (Table 20. 3), the pattern suggests that this ant's niche may be included in that of the other two species, and is dependent on rapid rates of resource supply. Davidson *et al.* (1990) have called attention to the commonness of similar included niche phenomena in relation to light environments of other terrestrial and epiphytic myrmecophytes (Huxley 1978; Janzen 1983; McKey 1984; Benson 1985; Jebb 1985; Harada and Benson 1988; Longino 1989a). As is often the case in other systems of included niches (reviewed in Colwell and Fuentes 1975), species dependent on abundant resources often survive by superior colonizing or competitive ability, while others persist by virtue of greater tolerance of less favourable environments.

Developmental differences between ants

The early resolution of competition has at least two important implications. First, there is a premium on rapid colony development if the requisite resources are available. This is suggested by the observation that colony (brood) size was greater on average for *Azteca ovaticeps* than for other specialized *Cecropia* ants six weeks after colonization of *C. membranacea* growing in full sun (D. W. Davidson and P. Herrera unpublished work). On slow-growing *C. membranacea* in the greenhouse, rapidly expanding col-

onies of *A. ovaticeps* destroyed new leaves by excavating immature Müllerian bodies from trichilia, and swarmed off the host plant in search of additional hosts.

Secondly, the resources determining the competitive outcome may be those available to foundresses, rather than to established colonies. The flight muscles of foundresses are often catabolized to provide resources for the first worker brood (Janet 1907; reviewed in Wilson 1971). With poorly developed flight muscles (relative to *Azteca xanthochroa*), *A. ovaticeps* queens may be especially dependent on the nutritional parenchyma lining internal walls of *Cecropia* internodes (Fig. 20. 5(a)).

Parenchymal thickness depends on host species and light intensity, the lining being best developed in host species growing regularly at high light intensity. *Azteca ovaticeps* queens transferred to saplings of *C. tessmannii*, which lacks the parenchyma, tended to die or desert at disproportionately high rates, or to produce smaller broods over a six-week period, than did queens transferred to *C. membranacea*, a host species with well-developed

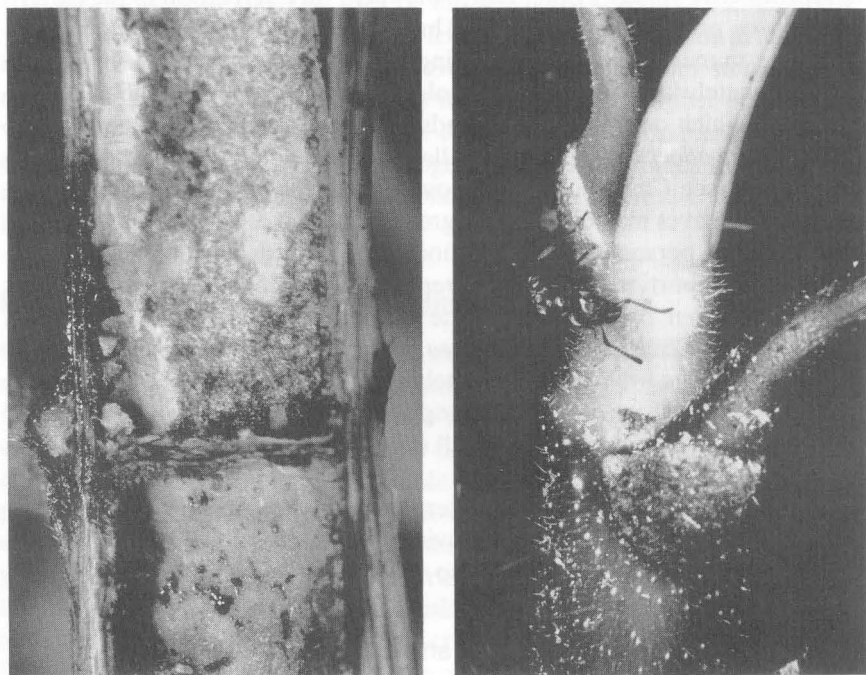


Fig. 20.5. (a) Thick parenchyma lines the internal walls of *Cecropia membranacea* stems in plants growing at high light intensities. Patches of this material have been removed by ant larvae. (b) *Pachycondyla luteola* queen investigates the prostoma of *Cecropia tessmannii*. The prostoma of this host is unique for its large size, outward swelling, and long, urticating hairs which exclude small *Azteca* queens.

parenchyma (D. W. Davidson and P. Herrera, unpublished work). In the *Cecropia* specialist *Pachycondyla luteola* (and the newly discovered *Pachycondyla* sp. nov. on Panamanian *C. hispidissima*), egg production by foundresses apparently depends on nutrition from unusually large Müllerian bodies, which queens themselves collect and store inside colonized internodes of the typical host, *C. tessmannii*. Of the six common host species, *P. luteola* queens colonize only two apparently close relatives (*C. membranacea* and *C. tessmannii*) with Müllerian bodies > 0.09 mg (Davidson *et al.* 1990). Queens transferred to *C. membranacea* deserted or died at higher rates than those transferred to *C. tessmannii*. When foundresses transferred to the typical host were sealed inside their internodes by corking prostomata, most of them either died or escaped by cutting new exit holes within two days of transfer. Queen dependency on Müllerian bodies may explain why the only two *Pachycondyla* species presently confirmed as *Cecropia* specialists are specific to hosts whose Müllerian body production is skewed to new leaves (Table 20. 2), safely accessible to queens occupying the newest internodes.

Later in colony life histories, interspecific differences in relative allocation to reproductive versus worker castes may also vary in relation to the pattern of resource provisioning by hosts. Thus, the ability of *Azteca ovaticeps* to dominate numerically on fast-growing hosts may also depend on its disproportionately large investment in colonizing reproductives. Unlike *A. xanthochroa*, which occupies and defends the entirety of its tree including the trunk, *A. ovaticeps* maintains smaller worker populations restricted to branch tips (see Chapter 19). Moreover, preliminary observations suggest that reproductives may constitute a greater fraction of total colony biomass (J. T. Longino, personal communication; D. W. Davidson, personal observation). The proportionately greater reproductive allocation of this species might have been predicted from the normally brief lifespan of its most common host, *Cecropia membranacea*, which is replaced in riverine succession at an average age of approximately ten years (Terborgh 1983). In contrast, *C. tessmannii* is a dominant canopy species on the edges of swamps and aguajals, and probably reaches its full stature (c. 35 m) only after several to many decades.

Figure 20. 4(c) summarizes our interpretation of correlations between ant traits and patterns of resource provisioning by hosts. The hypothesized implications for plant defence are also shown.

Competition between specialized and unspecialized ants

Competition may also influence the composition of ant-plant symbioses at later stages in their life histories. An example outside the *Cecropia* system is that of *Pheidole minutula*, which can take over branches of *Clidemia heterophylla* Steud. (Melastomataceae) from *Crematogaster cf. victima* when branches of their separate shrubs come into contact (Davidson *et al.* 1989).

The behaviour of attacking vines and other vegetation which is in contact with hosts may be an evolutionary response to competition from unspecialized, behaviourally dominant competing or predatory ants (Davidson *et al.* 1988). Pruning of vegetation is especially well developed in some pseudomyrmecine ants (e.g. Janzen 1966, 1972; Davidson *et al.* 1988) which create areas that are barren of vegetation around the host tree. Although none of the four specialized Peruvian *Cecropia* ants (Table 20. 3) makes distinct clearings around its hosts, all but *Camponotus balzani* prune vines to some extent (Davidson *et al.* 1988, 1990). Pruning is facultative in *P. luteola*, occurring only when vines are occupied by predaceous or competing ants (D. W. Davidson and P. Herrera, unpublished work). Perhaps because of pruning, there is no indication that unspecialized ants ever take over *Cecropia* hosts from specialized ants once colonies of the latter are established. Nevertheless, some ant species may be specialists on mature trees that have lost their previous residents (e.g. Benson (1985) for *Azteca schimperi*).

Many unspecialized ant species are occasional residents of *Cecropia* (Longino 1989a), usually inhabiting the lower trunks or seedling stems, and typically foraging off the host. In Peru, unspecialized species of *Camponotus*, *Crematogaster*, *Pachycondyla*, and *Solenopsis* are most common in the lower internodes of trees housing *Azteca ovaticeps* in their upper stems. These occasional *Cecropia* residents usually nest in a variety of other plant stems, with colonies often fragmented over different hosts. For reasons not yet clear, none of them appears to recognize Müllerian bodies as food. The necessity for foraging off the host plant may prevent these species from becoming *Cecropia* specialists.

Parasitoids might affect the competitive outcome

On both ecological and evolutionary time-scales, predation and parasitism may interact with competition to determine the distribution of alternative ant species in particular hosts and habitats. The evolutionary case would be especially difficult to detect (Bernays and Graham 1988). Since established ant colonies tend to be immune to mortality from predation and because host-plant ownership is resolved early in establishment, the most significant effects of predation and parasitism should be those affecting queens and young colonies. At Cocha Cashu, mortality due to parasitoids is highest for the most frequent colonists of *Cecropia membranacea*, the most abundant and conspicuous myrmecophyte in this region. In October 1988, beach seedlings were visited daily in order to date colonization of particular internodes. Six weeks after colonization, internodes were opened to reveal their contents. Based on conservative estimates, 21 per cent of *Azteca ovaticeps* queens were found to have been killed by parasitoids, most frequently *Conoaxima* sp. (Eurytomidae, Chalcidoidea). Members of this parasitoid genus apparently specialize in attacking *Azteca* foundresses (R. R. Snelling,

personal communication; Longino 1989a). Parasitoids may locate queens by searching for host plants; female *Conaxima* were observed to visit various seedlings, where they inspected newly sealed prostomata.

The brood of incipient *Pachycondyla luteola* colonies may be particularly easy targets for parasitoids because host prostomata are especially large, and are left open for queens to collect Müllerian bodies. As many as nine perilampid wasps (Perilampida, Chalcidoidea) can emerge from individual pupae of *P. luteola*. Present evidence is too preliminary to evaluate whether these and other parasitoids influence the distribution of specialized plant-ants in particular hosts and habitats.

Variation in host-plant protection by alternative ants

If alternative ants differ in the protection afforded to their hosts, then some of the ants may be parasites of relationships between these hosts and other ants. Among the four specialized *Cecropia* ants of Amazonian Peru, *Azteca xanthochroa* and *Pachycondyla luteola* are the most aggressive, racing down the trunk in response to the slightest disturbance. *Camponotus balzani* probably offers the least effective defence; this ant is extremely timid, principally nocturnal, and seldom ventures away from trichilia to patrol leaves. *Camponotus* may even directly injure its hosts by tending scale insects within stems. This practice would buffer variation in rates of resource provisioning and, perhaps, explain how this ant can inhabit so many host species (Table 20. 3). In contrast to Central American *Azteca*, the Peruvian species do not regularly tend Homoptera inside *Cecropia* stems.

Before classifying *Camponotus balzani* and/or *Azteca ovaticeps* as parasites, one must take into account other defences of host plants. Hosts with either short leaf lifetimes or chemical protection of mature leaves may require biotic defence only for young leaves. If this were so, then even relatively timid ants that foraged only at branch tips might proffer adequate defence. Additionally, if host fitness were most sensitive to herbivory at the seedling and sapling stages, then colony development rates may be as, or more, important than differences in ant behaviour in determining the benefits that different ants afford their hosts. Finally, parasitic ants might be most likely to invade ant-plant associations (and even to become specialized plant-ants) on hosts that provision ants in a way that permits timid ants to monopolize the food resource. Thus, both *P. luteola* and *Pachycondyla sp. nov.* (B. L. Fisher, personal observation) are specialized on hosts whose Müllerian body production is skewed toward the youngest leaves. *Pachycondyla* queens open partitions between internodes to colonize new internodes as these are produced. Trichilia are easily accessible to queens (and later workers) foraging through prostomata at the very tips of branches. If hosts do not require protection of older leaves, host evolution is less likely to oppose parasites and may even lead to increasing accommodation of these

new arrivals. Arguments like these may help to resolve the paradox of *Cecropia hispidissima* traits that seem to favour *Pachycondyla sp. nov.*, despite the reluctance of these timid ants to leave their stems except when foraging at the newest trichilia (B. L. Fisher, personal observation).

Habitat variation in herbivore pressures

Herbivore pressure doubtless varies with geography and habitat. Thus, although leaf-cutting ants are a major threat to *Cecropia* in many areas, they are rare and unimportant in the frequently flooded forests of south-eastern Peru. At Reserva Tambopata, herbivores of young *Cecropia* lacking trichilia included Coleoptera, Diptera, Hemiptera, Homoptera, and Orthoptera. Most abundant and devastating in large clearings with numerous *Cecropia* seedlings are *Coelomera* beetles (Coleoptera, Chrysomelidae) which are specialists on *Cecropia* (Andrade 1984; Jolivet 1987*b*, Chapter 26, this volume). These beetles were practically absent from isolated *Cecropia* saplings in small forest light gaps. Preliminary evidence suggests that *Coelomera* numbers vary with habitat rather than with (correlated) host species. The few shade-tolerant species sampled within large disturbances had beetle densities comparable to those on the light-demanding species. Herbivore pressure from *Coelomera* and other *Cecropia* specialists (Table 20. 4) may be low on plants in small isolated light gaps because the smaller seedling populations are more difficult to find, and are not sufficiently large or dense to support breeding populations of the herbivores. The relatively high investment by some shade-tolerant species in biotic defence (Table 20. 2) is even more noteworthy, given the comparatively low herbivore densities in their characteristic habitats.

Inferring determinants of evolutionary specialization

Our understanding of the factors leading to evolutionary specialization will depend on knowing which plants and ants have evolved traits that increase the species specificity of their relationships. Such traits are difficult to detect because ecological and evolutionary effects are confounded. Habitat specificity in the outcome of ecological processes (e.g. ant competition and parasitoid infection) may produce specific and repeatable patterns of ant association with particular habitats and hosts in the absence of evolved specificity. Experimental manipulations will be required to distinguish such species sorting (Jordano 1987) from special adaptation (Davidson *et al.* 1989).

Although existing data can suggest the distributions of evolutionary specialization leading to specificity, they cannot distinguish whether such specializations arose before or after symbiotic associations were common. The absence of *Azteca ovaticeps* foundresses from slow-growing, shade-tolerant

Table 20.4. Herbivory on natural populations of *Cecropia* seedlings lacking established ant colonies (at Reserva Tambopata, south eastern Peru).

<i>Cecropia</i> species	$n_p(n_L)$	All herbivores		Most common herbivores	
		H/P	H/L	H/P	H/L
Large disturbances (human clearings)					
<i>C. membranacea</i>	3 (24)	11.7	1.5	4.0	0.5 ^a
<i>C. engleriana</i>	16 (175)	8.2	0.8	3.5	0.3 ^a
<i>C. polystachya</i>	7 (47)	5.1	0.8	2.1	0.3 ^a
<i>C. tessmannii</i>	2 (15)	6.5	0.9	3.1	0.5 ^a
<i>C. species A</i>	1 (4)	2.0	0.5	2.0	0.5 ^a
Forest gaps					
<i>C. tessmannii</i>	21 (153)	0.3	0.0	0.1	0.0 ^b
<i>C. species A</i>	11 (85)	0.4	0.1	0.3	0.0 ^c
<i>C. ficifolia</i>	11 (75)	0.6	0.1	0.4	0.1 ^d

* n_p = number of plants sampled per species; n_L = number of leaves sampled per species; H/P = mean number of herbivores per plant; H/L = mean number of herbivores per leaf. Herbivores varied markedly in type and number on individual seedlings and no statistical analysis is attempted. Rigid habitat associations of plants restricted our sample sizes of plants in uncharacteristic habitats.

^{a-d} Most common herbivores of various *Cecropia* species: a = *Coelomera* sp. (Coleoptera, Chrysomelidae), accounting in large disturbances for 35 per cent of herbivores of *C. membranacea*, 43 per cent of those on *C. engleriana*, 42 per cent of those on *C. polystachya*, 54 per cent of those on *C. tessmannii*, and 100 per cent of those on *C. species A*. In forest light gaps, b = any of 6 herbivores represented by a single individual *C. tessmannii*; c = Coleoptera sp. 3, accounting for 75 per cent of herbivores on *C. species A*; d = Coleoptera sp. 4 (Curculionidae), comprising 57 per cent of herbivores on *C. ficifolia*.

Cecropia (Table 20. 3) implies either host or habitat specificity. This species (probably a species group, Longino 1989a, b) became a *Cecropia* specialist independently of at least three other major radiations of *Azteca* onto *Cecropia* (Benson 1985; Longino Chapter 19, this volume). Habitat-specific searching could have arisen prior to specialization on *Cecropia* if this species were dependent on the high productivity of early successional habitats. Similarly, rapid colony development, early and high reproductive allocation, and short queen lifespans may have been pre-adaptations for the present lifestyle as a colonizing species. However, both habitat and host-restricted searching and traits related to the occupation of fast-growing hosts could have originated as responses to differentially high fitness on *Cecropia* with high rates of resource provisioning. Preferences may also have evolved for hosts whose favourable resource environments allowed

rapid growth and high leaf turnover to compensate for herbivory. In *Pachycondyla luteola*, host specificity appears more likely than habitat specificity, because the species colonizes only two, probably closely related, species of *Cecropia* in different environments. Nevertheless, to determine confidently whether either *Azteca ovaticeps* or *P. luteola* have specialized on particular habitats or hosts, colonization must be observed on hosts transferred experimentally to uncharacteristic habitats. Observations of queens transferred to atypical hosts would show whether ants have evolved preferences for certain hosts, or whether the unused host species are adapted to exclude particular ants.

Indications that host trees may specialize on particular ants are strongest for slow-growing, shade-tolerant species, which should have the most to lose by housing ants that provide inferior protection. First, in *Cecropia tessmannii*, long urticating hairs on an enlarged and outwardly swollen prostoma (Fig. 20. 5(b)) exclude small *Azteca* queens, which apparently never colonize these plants. At least, *A. xanthochroa* foundresses search in habitats where *C. tessmannii* seedlings volunteer, and experimentally transferred *A. ovaticeps* queens attempt unsuccessfully to enter these prostomata (D. W. Davidson and P. Herrera, unpublished work). Although *A. xanthochroa* colonies appear to afford excellent protection to their hosts, low rates of resource provisioning by this especially slow-growing host may frequently lead to the mortality of incipient colonies and, thus, a delay in the host's acquisition of biotic defences. Secondly, the very narrow and short internodes of *Cecropia* sp. A may exclude large queens of both *Camponotus balzani* and *Pachycondyla luteola*. These queens appear not to colonize *Cecropia* sp. A despite their presence in other shade-tolerant hosts (Table 20. 3). Especially low leaf tannin concentrations (see above) and disproportionately high reliance on biotic defence (Table 20. 3) may make this species particularly susceptible to herbivory when housing *C. balzani*.

There are other indications that *Cecropia* species have specialized to particular ants. Müllerian bodies of *C. tessmannii* are unusually large, averaging approximately three times the dry weight of those on *Cecropia* species that typically house small *Azteca* ants, and almost twice as large as those of *C. membranacea* (Davidson *et al.* 1990). Comparatively large *P. luteola* workers will collect the smaller food bodies when these are supplied artificially from other plants, but queens regularly reject them. *Pachycondyla* sp. nov. is even larger in size and the Müllerian bodies of *C. hispidissima* may be larger and harder than those of any other *Cecropia* species (as well as being purple!). Subtle differences in Müllerian bodies are almost certainly more apparent to ants than to human observers. In the greenhouse, we successfully colonized *C. ficifolia* with *A. ovaticeps*, an ant which never occurred on this host in the field (Table 20. 3). Here, in contrast to their frenzied activity on other hosts, workers were lethargic, standing motionless on or near trichilia with mandibles often open, as in an 'attack posture'.

Although the workers did collect some Müllerian bodies, many remained pendant on the trichilia and eventually fell.

Finally, Berg (1978*b*) suggested that the tiny stem hairs of *Cecropia* function as 'ladders', giving sturdy footing to attendant ants. In this context, it is interesting that dense stem hairs are much longer (2 mm) on *C. tessmannii* and *C. hispidissima*, which regularly house the large *Pachycondyla*.

Defence-mediated speciation in *Cecropia*, an hypothesis

Ant-plants wear their defences on the outside, and patterns in defence investment are more easily observed than in chemically defended plants. One remarkable pattern stands out for the western Amazonian *Cecropia*. Defensive investment changes with habitat in similar ways for the three pairs of probable close relatives. If phylogenetic evidence supports the hypothesis that closest relatives inhabit different light environments, then plants may have speciated across habitat boundaries, perhaps by mechanisms related to defence investment. *Cecropia* trees produce numerous small seeds, dispersed widely by mobile vertebrates (birds, bats, and monkeys; reviewed in Holthuijzen and Boerboom 1982). Many of these seeds regularly reach atypical environments and genetic variation in anti-herbivore defence systems would be tested each year in habitats differing in herbivore pressure and availability of plant resources. Variation in defence investment could occasionally permit saplings to survive in otherwise unsuitable habitats, especially if isolated plants experienced lower herbivore pressure (e.g. Feeny 1970).

At maturity these *Cecropia* might be reproductively isolated by differences in flowering season; intraspecific variation in reproductive season of one *Piper* species is known to be influenced by light regime (Marquis 1988). Among the six *Cecropia* species, light-dependent *C. membranacea* and *C. engleriana* flower and fruit in the wet season but each of their probable close relatives reproduces in the dry season, when the photosynthate needed to fill fruits may be less limiting to these often shaded plants. Although *C. polystachya* and *C. ficifolia* both fruit in the wet season, fruiting seasons are slightly displaced, but flowering times are not yet known. The hypothesis of sympatric (but not syntopic) speciation in relation to evolutionary tradeoffs between defence and growth need not be restricted to myrmecophytes, but could generalize to other tropical plants with small and widely distributed seeds. This hypothesis is consistent with Gentry's (1989) view that habitat specialization (principally in vegetative traits) has been of great importance to speciation in Amazonian rainforest plants.

***Cecropia* as a model for studying ant-plant symbioses**

Locally high species diversities of both *Cecropia* and its specialized ants make this system particularly complex, though perhaps not uniquely so given

superficial convergences with the *Macaranga-Crematogaster* association in Asia (see Chapter 18). With complexity comes opportunity to move from a purely descriptive to an explanatory phase in the study of ant-plant symbioses. Patterns in the allocation of plant defence investment may be useful in predicting rates and patterns of resource supply to symbiotic ants. In turn, interspecific differences in resource supply may determine both the identities of ant associates and adaptations of both ants and plants to one another. Where variation in the species composition of ant-plant associations is possible, given the evolved attributes of plants and ants, associations may be determined by the sometimes habitat-specific outcome of competition among specialized ants for hosts. The competitive outcome might occasionally be modified by foundress mortality from parasitoids.

The selection environments of symbiotic ants and plants are multivariate and must be characterized fully before we can answer the kinds of questions posed by A. J. Beattie in Chapter 37. Relationships may be mutualistic or not, depending on the protection proffered by alternative and competing ants, the growth rates, leaf lifetimes, and alternative defences of various congeneric hosts, and subtle changes in plant resources across habitat boundaries. If the selection environment is not well characterized, even the most straightforward predictions set out for expensive and time consuming tests of micro-evolutionary hypotheses may be completely wrong. The evaluation of a pattern within these highly context-dependent associations may also provide the best means of identifying mechanisms that both promote and oppose the diversification of symbiotic ant and plant species.

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