Mosaic Ant Territories in an African Secondary Rain Forest (Hymenoptera: Formicidae)

by

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ABSTRACT

A comparison was made of the distribution of ant species in two man-made formations: an old secondary forest and the forest edge. This forest was composed of two kinds of trees: trees belonging to the mature forest prior to clearing and trees of the secondary forest which grew after clearing. The former were occupied by *Crematogaster depressa*, a forest dwelling species which tolerated numerous nondominant ants in its territories. The others were occupied by the same species and *Atopomyrmex mocquerisi*, *C. clariventris*, *Pheidole* sp. (*megacephala* group), *Tetramorium aculeatum* and *Oecophylla longinoda*. One tree was occupied by a society of *Tetraponera anthracina*, another by *Polyrhachis militaris*, two species not previously known as dominant, and corresponding here to the subdominant status. These species occupied non-overlapping territories distributed in a mosaic as known in African tree plantations.

The forest edge was composed of plants at the pioneer stage. Dominant ant territories are not adjacent and numerous dominant species tolerated nondominant ants in their territories. This situation favored a high diversity of nondominant ants. As a result, large societies of *T. anthracina*, *Cataulachus guineensis*, *Camponotus brutus* and *Polyrhachis laboriosa* were able to demonstrate dominant-like behavior so that the species can be classified as having subdominant status.

Key words: arboreal ants, mosaic, secondary forest, Africa.

INTRODUCTION

In the tropical rain forest and tree crop plantations, dominant ants (species which predominate in an area, to the exclusion of other dominant ants) form a three-dimensional patchwork of non-overlapping territories called ant mosaics. Dominant arboreal ants found both in orchards and in the natural environment are of great interest because they influence the distribution and in consequence the abundance of

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other taxa, including other ants (Leston 1973, 1978; Majer 1986; Majer & Camer Pesci 1991).

In tree crop plantations, the manipulation of ant mosaics can be utilized in pest control (Majer 1976a, b; 1986), while studies on natural ecosystems permit us to have data on their influence in community organization and diversity, and on coevolutionary processes (Wilson 1958, 1959, 1987; Leston 1978; Gilbert 1980).

According to Majer (1972, 1986), we can distinguish four statuses in arboreal ant communities.

1. Dominant: species characterized by intra- and interspecific territoriality.

2. Codominant: in certain circumstances, two dominants coexist, having generally different rhythms of activity.

3. Subdominant: species which can reach dominant status under certain conditions, such as a more favorable environment. For example, *Camponotus acvapimensis* occur in isolated pockets, in the gaps between the adjacent territories of dominant ants, where the species is at its highest density in the immediate proximity of the nest.

4. Nondominant: species with small colonies which occur within or between the territories of dominants. According to Room (1971, 1975) and Taylor (1977), dominants have distinct communities of nondominants associated with them. In consequence, nondominant ants are also distributed in a mosaic pattern.

In Africa, ant mosaics were found in numerous tree crop plantations (Leston 1973, Majer 1976a, b, Taylor 1977, Bigger 1981, Jackson 1984, Dejean *et al.* 1991, 1993), but there is little published information on observations performed in the forest. At least in cocoa plantations, the ecology of African dominant ants is relatively well known, but nondominant ants are much less well known, although some of them are important predators of pests that the dominant ants do not attack (Way *et al.* 1989). Way & Khoo (1992) suggest that research on nondominant ants remains a challenge for the future.

In this study, we made a comparison between a parcel of very old secondary forest and the edge of this forest, along a dirt road. We asked the following 5 questions:

1. Is there a difference between dominant ant species occupying the secondary forest and those occupying the forest edge?

2. Is there a difference between dominant ant species occupying forest trees left after clearing, to act as shade and those occupying trees that grew after clearing?

3. Is it possible to show a correlation between certain ant species and certain tree species or certain types of plant communities?

4. Is it possible to show that distinct communities of nondominant ants are associated with dominants?

5. Are these perturbed habitats favorable to the installation of subdominant ants?

If yes, is it possible to outline the conditions which permit these ants to compete with dominants to get a specific territory?

METHODS

Study area

This study was undertaken in January 1991, next to the village of Matomb-Brousse, 65km west of Yaoundé on the road to Douala (3°50'N; 11°2'E; 500m alt.), in an area with an annual rainfall of 2200mm (Suchel 1965). In this area, old secondary rain forest is found interspersed with cocoa tree, cassava, and plantain plantations.

Data in the secondary forest were collected when farmers cleared a trapezoidal parcel of about 7,800m^2 (Fig. 1). We had thus the possibility of directly inspecting the canopy of the trees, immediately after they were cut down. Note that this was an opportunistic strategy; the trees would have been cut anyway by the farmers who needed more agriculture land to accomodate a greater rural population due to a decrease in rural-urban migration related to the economic crisis affecting towns. For comparison, we decided to inspect plants of more than 1m high along both sides of the dirt road which cut through the forest. The area was 5m wide on each side of the road, 1km long: 10,000m^2 in theory, but we estimated that plants of more than 1m high occupied around 80% of this area. These plants, situated along the forest edge seek exposure to the sun.

Methods of mapping tree and ant species distributions

Each tree whose top reached the canopy of the forest was coded and mapped in a manner permitting us to determine its place. After the trees were cut down we noted their lengths and the diameters of their trunks at the level of the cut. Then, we took samples of leaves, branches, bark and wood, also flowers and fruits when possible, in order to make determinations at the laboratory. The determinations were made in coordination between two of the co-authors (A.D. & A.A.) and different specialists of the National Herbarium and of the forestry centre of the Research Institute of Agriculture of Cameroon.

Just after each tree was cut down, most of the ants ran on branches and foliage permitting us to note easily the presence of not only dominant species but also nondominant (often discrete) species. The extent of the territories of dominant ants was easy to evaluate by direct

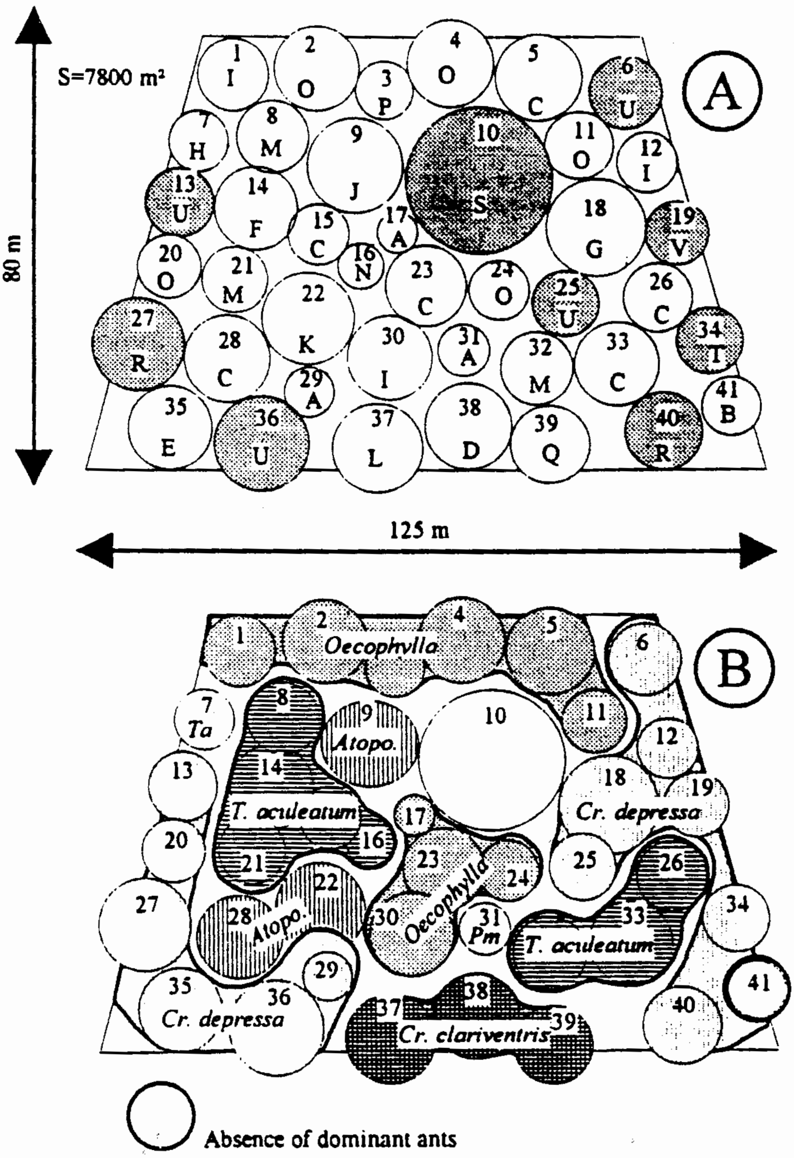

Fig. 1. Representation of the parcel of secondary forest. A: distribution of the trees in the parcel; in grey, trees of the mature forest left for shade after clearing which happened 60 years ago; the letters correspond to tree species according to a code presented in Table 1. B: distribution of the dominant ant territories. Two trees, n° 10 and 41 were not occupied by dominant ants; the tree crowns were occupied by only one dominant or subdominant species with an exception: a small part of the foliage of the tree n° 22 was occupied by *Crematogaster depressa* while on the rest of the tree nested a society of *Atopomyrmex mocquerisi*. We found two cases of subdominantspecies: *Tetraponera anthracina* (Ta) on tree n° 7 and *Polyrhachis militaris* (Pm) on tree n° 31.

observation. Of the dominants which build nests with carton and/or leaves (*Crematogaster clariventris*, *C. depressa*; *Tetramorium aculeatum*, *Oecophylla longinoda*), we studied not only the nests (polydomus societies), but also the peripheral shelters where they tend homopterans and/or they temporarily place their prey. We located nest entrances of *Atopomyrmex mocquerisi*, a carpenter ant, on peripheral branches, cut several branches with machetes and looked for zones where they tend homopterans. We peeled the bark off of branches to determine the extent of the nests of *Pheidole* sp.

To test if ants of the same species installed on different trees belonged to the same society or not, we introduced workers taken from one tree onto the foliage of another tree where the same species was found. Introduced workers can be accepted (same society; generally adjacent trees) or attacked and killed (two different societies).

We looked for the nests of nondominant ants in the foliage and on large branches, particularly when we found necrosis, dead branches and epiphyte ferns and orchids. We captured them in glass tubes through the use of an aspirator. The crown of the palm-trees (*Elaeis guineensis*) contains many cavities where ants can nest, so we decorticated the zone where the leaves were attached to reach the ant societies.

When the ant species determinations were not obvious, samples of ants were put into glass tubes containing 60° ethanol and sent to B. Bolton.

For the work along the forest edge, we registered the succession of plants of more than 1m high on pre-drawn maps. The determination of these plants was generally obvious. A species-level identification necessitated taking certain of the samples to the National Herbarium for comparison. Identification was made only at the genus level for four species (young individuals). For *Costus albus* and *Alchornea cordifolia* the mapping corresponds to groups occupying places of variable size, sometimes greater than 10m, along the road.

Associated ants were registered during mapping with the following distinctions: 1) status of dominant or nondominant, 2) nesting in the trees sampled, 3) only foraging on their foliage. Arboreal nests were easy to locate; we also penetrated systematically into the brushwood to find nests that were hidden. To find nests of other species, we broke open with a machete each dead branch (remaining on the trees or laying on the soil) and stripped the bark in places where it was cankered. This strategy permitted us to locate nests of nocturnal species such as *Pheidole* sp. and *Camponotus brutus*. When we were unsure of a species, we took samples in ethanol for later determination.

RESULTS AND DISCUSSION

The Parcel of Old Secondary Forest

The parcel where we worked was characterized by the presence of only large trees (Fig. 1; Table 1) that we divided into three categories, lianas being absent.

1) Trees of the secondary forest (or pre-climacic stage census, Kahn 1982; see also Schnell 1976; Fournier & Sasson 1983). With the exception of a *Canthium* sp. (20m high) probably broken by a very large branch falling down from an adjacent *Albizia zygia*, these trees were between 35 and 40m high, including the palm trees. The diameters of their trunks varied from 60cm (a palm tree) to 140cm (an *Albizia zygia*). Note the presence of a large-sized *Musanga cecropioides* (Fig. 1: n° 35) that we included in this category although theoretically it belongs to pioneer formation. It is known that the longevity of isolated individuals is superior to that of dense monospecific communities.

We can have an idea of the age of certain tree species by comparing the data of Kahn (1982). The trees of our parcel had reached their maximum height (between 30 and 40m). The diameters of the trunks of 40 year-old *Fagara macrophylla* were around 80cm, versus 90-110 cm for those in our parcel; 60 year-old *Albizia zygia* had trunks of 120 cm versus 140cm for one in our parcel; 60 year-old *Terminalia superba* had trunks of 55cm versus 90cm for one in our parcel. We estimate that the trees of the secondary community in the studied parcel had reached their maximum size (height and diameter of the trunk) and were about 60 years old.

2) Among the trees of the mature forest (or climacic forest; Kahn 1982) the largest one, *Microberlinia bisulcata* had a height of more than 50m, its trunk was 2.5m in diameter at the level of the cut; and the tree top had a projection to the soil of about 500m^2 (some lateral branches reached more than 15m from the axis of the trunk; Fig. 1: n° 10). The other trees, had a height of 30-45m; the diameters of their trunks, at the level of the cut being 90-140cm. These trees are characterized by slow growth, and the necessity for shade when young, and are very old compared to those of the secondary forest. We deduce that they were left in place by the farmers during clearing (which happened about 60 years ago).

3) *Anthiaris africana* and *Homalium letestui* can grow in both secondary and mature forests. We found one sample of each species with heights of about 35m, the diameters of their trunks being 70cm for *A. africana* and 80 cm for *H. letestui*. It is very probable that they grew after the forest was cleared.

Table 1. Tree-dominant ant species relationships in the old secondary forest. (W): without dominant ants; (SUBDOM.): subdominant species; (*): a nest of *Platythyrea conradti* (Ponerinae) under epiphyte fern; (Cc): *Crematogaster clariventris*; (Cd): *Crematogaster depressa*; (Tac): *Tetramorium aculeatum*; (Oec): *Oecophylla longinoda*; (Ta): *Tetraponera anthracina*; (Ato): *Atopomyrmex mocquerisi*; (Phe): *Pheidole megacephala*; (Pm): *Polyrhachis militaris*; (TOT.): TOTAL.; (¹): trees of the primary or mature forest; (²): typical trees of the secondary forest cited by Schnell (1976). *Anthiaris africana* and *Homalium letestui* can grow in the two kinds of forest. The letters at the left edge of the table correspond to a code for the placement of each tree species in Fig. 1.

	TREE SPECIES	W	DOMINANT ANT SPECIES						SUBDOM.		
			Ato	Crc	Crd	Phe	Tac	Oec	Ta	Pm	TOT
	ARECACEAE										
A	*Elaeis guineensis*[2]	.	.	.	1	.	.	1	.	1	3
	ANACARDIACEAE										
B	*Lannea welwitschii*[2]	1	.	.	.	.	.	.	.	.	1
	APOCYNACEAE										
C	*Alstonia boonei*[2]	.	1	.	.	.	3	2	.	.	6
D	*Rauvolfia macrophylla*[2]	.	.	1	.	.	.	.	.	.	1
	CECROPIACEAE										
E	*Musanga cecropioides*[2]	.	.	.	1	.	.	.	.	.	1
F	*Myrianthus arboreus*[2]	.	.	.	.	.	1	.	.	.	1
	COMBRETACEAE										
G	*Terminalia superba*[2]	.	.	.	1	.	.	.	.	.	1
	LAURACEAE										
H	*Beilschmiedia zenkeri*[2]	.	.	.	.	.	.	.	1	.	1
	LECYTHIDACEAE										
I	*Petersianthus macrocarpus*[2]	.	.	.	.	1	.	2	.	.	3
	MIMOSACEAE										
J	*Albizia sp.*[2]	.	1	.	.	.	.	.	.	.	1
K	*Albizia zygia*[2]	.	1	.	.	.	.	.	.	.	1
	MORACEAE										
L	*Ficus exasperata*[2]	.	.	1	.	.	.	.	.	.	1
	MYRISTICACEAE										
M	*Pycnanthus angolensis*[2]	.	.	.	.	.	3	.	.	.	3
	RUBIACEAE										
N	*Canthium sp.*[2]	.	.	.	.	.	1	.	.	.	1
	RUTACEAE										
O	*Fagara macrophylla*[2]	.	.	.	1	.	.	4	.	.	5
	MORACEAE										
P	*Anthiaris africana*	.	.	.	.	.	.	1	.	.	1
	SAMIDACEAE										
Q	*Homalium letestui*	.	.	1	.	.	.	.	.	.	1
	CESALPINIACEAE										
R	*Distemonanthus benthianus*[1]	.	.	.	2	.	.	.	.	.	2
S	*Microberlinia bisulcata*[1]	1*	.	.	.	.	.	.	.	.	1
	ERYTHROXYLACEAE										
T	*Erythroxylum mannii*[1]	.	.	.	1	.	.	.	.	.	1
	IRVINGIACEAE										
U	*Desbordesia glaucescens*[1]	.	.	.	4	.	.	.	.	.	4
	STERCULIACEAE										
V	*Pterygota sp.*[1]	.	.	.	1	.	.	.	.	.	1
	TOTAL:	2	3	3	12	1	8	10	1	1	41
	PERCENTAGES:	4.9	7.3	7.3	29.3	2.4	19.5	24.4	2.4	2.4	

The Edge of the Forest

It was characterized by the predominance of *Costus*, *Alchornea* and *Macaranga* spp. (Table 2), three groups that are among the principal components of the pioneer shrubby stage (Kahn 1982). With the exception of *Anthocleista vogelii*, other species were young forms of secondary trees always present at this stage (Schnell 1976; Kahn 1982). *A. vogelii* is a species of the ripicolous forest that Kahn (1982) encountered only in certain parcels where it promoted a rapid reconstitution of the forest when forming communities.

The area studied, situated at the bottom of a hill, is humid and probably favors the presence of high densities of *Costus albus* and *Alchornea cordifolia*, and in consequence has low plant diversity. *C. albus* developed in patches which totaled 820m along the 2000m of forest edge (41%), while patches of *A. cordifolia* developed on 1350m (67.5%). Frequently, these two plants were concomittant, *Costus* being at the exterior, *Alchornea* against the forest trees, forming a scar area along the forest edge.

In such situations, the diversity of plants whose foliage was in direct sunlight was superior in the parcel of forest than at the forest edge (17 families/22 species/41 individuals versus 10 families/14 species/343 individuals), the difference is highly significant (ε=12>6.1; $P<10^{-9}$).

In other places along this dirt road, we noted the presence of other species forming monospecific patches such as *Aphramomum* and *Costus* spp. (Zingiberaceae), *Musanga cecropioides* (Cecropiaceae), *Trema guineensis* (Tilliaceae) and *Chromolaena odorata* (an imported Asteraceae); we also found groups of *Barteria fistulosa* (Passifloraceae, a myrmecophyte associated with *Tetraponera aethiops*).

The Dominant Ant Mosaic

1) The secondary forest

Of the 41 trees cut down in the forest, 37 (90.2%) were occupied by dominant ants (Table 1); 2 others were occupied by very large societies of ants not previously known as dominant species (4.9%); and the last two (4.9%) were not occupied by ants with dominant-like status. The territories of dominant ants were obvious to determine, each tree being occupied by only one dominant ant species, with one exception: a part of the foliage of an *Alstonia bonei* sheltering *Atopomyrmex mocquerisi* was occupied by workers and periphery shelters of carton of *Crematogaster depressa* whose nests were settled in the adjacent trees (Fig. 1, n° 28).

Tests of agressivity permit us to show that workers of the same species installed on adjacent trees tolerated each other in each case. To the contrary, workers of *Crematogaster depressa*, *Tetramorium aculeatum*

Table 2. Ant species nesting on plants of more than 1m high on both sides of 1km of dirt road that crosses the secondarized rain forest, between Matomb and Matomb-brousse. (*Cra*): *Crematogaster stadelmanni*; (*Crs*): *Crematogaster striatula*; (*Phe*): *Pheidole megacephala*; (*Tac*): *Tetramorium aculeatum*; (*Oec*): *Oecophylla longinoda*; (*Pl*): *Polyrhachis laboriosa*. (**): groups of the same plant; (*): nesting in the inflorescences of *Costus alba*.

PLANT SPECIES	WITHOUT NEST	DOMINANT	ANT	SPECIES			NON-DOM.	TOTAL
		Cra	*Crs*	*Phe*	*Tac*	*Oec*	*Pla*	
ZINGIBERACEAE (MONOCOT.)								
*Costus albus***	79	.	16*	17*	3	2	.	117
ASTERACEAE								
Vernonia conferta	2	.	.	2	1	1	.	6
CECROPIACEAE								
Myrianthus arboreus	8	.	.	.	1	.	.	9
COMBRETACEAE								
Combretum sp.	3	.	.	.	.	4	2	9
EUPHORBIACEAE								
*Alchornea cordifolia***	92	.	.	.	3	12	9	116
Bridelia micrantha	12	.	.	.	1	2	.	15
Macaranga hurifolia	16	.	.	.	.	5	1	22
Macaranga sp.	11	.	.	.	.	.	.	11
FLACOURTIACEAE								
Caloncoba welwitschii	1	.	.	.	.	2	.	3
LOGANIACEAE								
Anthocleista vogeli	2	.	.	.	2	1	.	5
MIMOSACEAE								
Albizia sp.	7	.	.	.	.	.	.	7
Albizia zygia	10	.	.	.	1	2	4	17
RUBIACEAE								
Canthium sp.	1	1	1	.	.	.	.	3
Morinda lucida	.	1	.	.	.	.	.	1
RUTACEAE								
Fagara macrophylla	.	.	.	.	.	2	.	2
TOTAL:	244	2	17	19	12	33	16	343
PERCENTAGE:	71.1	0.6	4.9	5.5	3.5	9.6	4.7	

and *Oecophylla longinoda* issued from two zones separated by territories of other dominant species do not tolerate each other. The workers of *Atopomyrmex mocquerisi* of the two zones (*Abizia* sp. on one hand; *Albizya zygia* and *Alstonia bonei* on the other hand; see Fig. 1, n° 9, 22 and 28) tolerated each other. It is probable that trails installed on the soil connected these two zones. We had therefore the opportunity to determine the territories of the different dominant ants (Fig. 1b) which are distributed in a mosaic pattern as in tree crop plantations.

It seems that ant species do not occupy the different tree species at random. For instance, *C. depressa* occupied 8 out of 9 of the trees of the primary forest versus 4 out of 29 of the secondary forest (difference highly significant: χ^2_c=14.6>10.8; P<0.001), while *T. aculeatum* and *O. longinoda* were encountered only on trees of the secondary forest, the last species occupying 4 out of 5 *Fagara macrophylla*.

The two trees (*Beilsthmiedia zenkeri* and a palm tree; see Fig. 1, n° 7 and 31) occupied by ants not previously known as dominant, sheltered respectively *Tetraponera anthracina* (Pseudomyrmecinae) and *Polyrhachis militaris* (Formicinae). Both species were considered as nondominant in cocoa plantations by Majer (1976b) and Taylor (1977). After having fallen, the foliage of the *Beilsthmedia* was covered by running workers of *T. anthracina*, which corresponds to several thousand ants. We tried to capture the entire society of *P. militaris* living between the bases of the leaves of the palm tree and estimated the population of workers at about 5000 individuals (4350 counted). Both societies were in a situation corresponding to the status of subdominant (populous and absence of dominant on the tree crown that they occupied).

2) The forest edge

Dominant ants belonging to 5 species nested on 83 plants sampled from the 343 counted in the area (24.2%; Table 2). The two *Crematogaster* species present there were different from those of the forest. *C. stadelmanni* built friable carton nests on the trunks of trees at the forest edge, while *C. striatula* is known to inhabit hollowed, dead branches, crevices, and cavities situated between wood and bark, but here it lived mostly in dry twigs and in inflorescences of Zingiberaceae. *Pheidole megacephala* compete with *C. striatula* to occupy the Zingiberaceae. *T. aculeatum* and *O. longinoda* seem to compete for different plants (note that the two *Fagara macrophylla* present were occupied by *O. longinoda*).

Due to the small size of the plants of this formation, the territories of the three dominant ants extended onto plants adjacent to those on which they nested. (*C. striatula* nested on 17 plants, had territories which extended onto 65; the ratio for other ants being: *C. stadelmanni*: 2/15 and *O. longinoda*: 33/43 (Tables 2 & 3). *P. megacephala* and *T. aculeatum* had their territories only on the plants on which they nested. Two terrestrial nesting species had territories at the forest edge: *Myrmicaria opaciventris* (Myrmicinae) and *Camponotus acvapimensis* (Formicinae) were both foraging in plants' foliage for extrafloral nectar, the honeydew of homopterans, and prey. *C. acvapimensis* is known as subdominant able to have territories in well insolated zones (Majer 1972), while *M. opaciventris* develops supercolonies that extend their influence over very large territories, particularly on fallow lands (Suzzoni *et al.* 1994).

3) Finally, it appeared that 135 plants out of 343 (39.3%) did not correspond to territories of dominant ants (Table 3). The situation was therefore very different than that observed in the secondary forest and in plantations where trees not occupied by dominant ants were rare.

Among the ant species which exploit these zones, some very large societies (and not others) were obviously territorial on certain plants.

Table 3. Relationship between dominant and nondominant ant species on the plants bordering the track. The first series of numbers corresponds to plants that composed the different zones and territories. (*Cra*): *Crematogaster stadelmanni*; (*Crc*): *C. clariventris* (1 hard carton-nest on the trunk of a tree situated behind the bushes bordering the track); (*Crs*): *C. striatula*; (*Phe*): *Pheidole megacephala*; (*Tac*): *Tetramorium aculeatum*; (*Oe*): *Oecophylla longinoda*; (*Mo*): *Myrmicaria opaciventris*; (*Ca*): *Camponotus acvapimensis*; (*Pl*): *Polyrhachis laboriosa* (for comparison; we took data on trees on which they have their nests); (*): nocturnal species.

NON-DOMINANT ANT SPECIES	WITHOUT DOMINANT	DOMINANT ANT SPECIES						GROUND			
		Cra	Crc	Crs	Phe	Tac	Oe	Mo	Ca	Pl	TOT
	135	15	19	65	19	12	43	16	3	16	343
PONERINAE											
Odontomachus troglod.	3	.	.	.	.	.	.	.	.	.	3
PSEUDOMYRMECINAE											
Tetraponera anthrac.	32	4	3	8	9	1	.	4	1	1	63
Tetraponera sp.	3	.	.	1	1	.	.	1	.	.	6
MYRMICINAE											
Cataulachus guineens.	17	1	2	2	4	.	.	1	.	2	29
Cataulachus sp.	11	2	1	3	2	1	1	1	.	1	23
Crematogaster sp.	11	.	2	.	3	.	.	1	.	.	17
Oligomyrmex sp.	2	.	.	.	.	1	.	.	.	.	3
Pheidole megacephala	22	1	.	2	/	1	1	2	1	1	31
DOLICHODERINAE											
Tapinoma melanocephala	1	.	.	.	1	.	.	1	.	.	3
Tapinoma sp.	.	.	2	1	1	.	.	.	.	.	4
Technomyrmex sp.	1	.	.	.	.	.	.	.	.	.	1
FORMICINAE											
*Camponotus brutus**	5	.	.	1	.	1	.	1	.	.	8
Camponotus chrysurus	2	1	1	1	.	.	.	2	1	.	8
Camponotus sp.A	19	2	2	5	7	1	1	1	.	1	39
Camponotus sp.4	2	.	.	2	1	.	.	.	.	.	5
Paratrechina sp.	2	1	.	1	.	.	2	1	.	.	7
Phasmomyrmex sp.	1	.	.	.	.	.	.	.	.	.	1
Polyrhachis laboriosa	11	1	2	5	4	1	4	2	1	/	31
Polyrhachis militaris	.	.	1	1	1	.	.	.	.	.	3
Polyrhachis weissi	3	.	.	.	.	.	.	.	.	.	3
TOTAL:	148	13	16	33	34	7	9	18	4	6	288
PERCENTAGES:	109.6	86.7	84.2	50.7	178.9	58.3	20.9	112.5	133	37.5	84

Statistical comparisons of percentages from contigency tables: *Oe/Crs*: χ^2_c=7.3>3.8; P<0.05; *Oe/Tac*: χ^2_c=6.7>3.8; P<0.05; *Tac/Crs*: χ^2_c=0.2<3.8; NS; *Crs/Crc*: χ^2_c=8.4>3.8; P<0.05; *Crc/Phe*: χ^2_c=5.8>3.8; P<0.05; *Crc/Mo*: χ^2_c=0.5<3.8; NS; *Pl/Crs*: χ^2_c=1.0<3.8; NS; *Pl/Oe*: χ^2_c=1.5<3.8; NS (*Pl*: trees on which they nest).

They had dominant-like behavior which corresponds to the status of subdominant. It was the case for 2 societies of *Tetraponera anthracina*, nesting in hollowed branches and twigs. This result reinforces those obtained in the secondary forest. It was also true for one society of *Cataulachus guineensis* (Myrmicinae) nesting in hollowed branches or in abandoned termitaries and two societies of *Polyrhachis laboriosa*, a Formicinae which builds nests in the foliage of trees and has polydomous societies. Finaly there was one society of *Camponotus brutus* (Formicinae nesting in dead branches, sometimes terricolous; the status of dominant previously observed by Room 1971).

The synthesis of Bigger (1981), the data of Jackson (1984) and Dejean *et al.* (1991) on the frequency of dominant ants in the canopies of African cocoa plantations, the preliminary data on the mature forest of south Cameroon (Dejean *et al.* 1992), and present results permit us to discuss the exact status of the most frequent dominant species.

C. depressa is a forest dwelling species. It was the only dominant species found in the trees of the mature forest left during clearing in the present study and by far the most frequent in the mature forest of south Cameroon. In cocoa plantations, it originates from trees left for shade.

O. longinoda, which was rare but present in the canopy of the mature forest of south Cameroon, was the most frequent ant in the trees characterizing the secondary forest and the plants of the pioneer stage (forest edge) in the present study. In cocoa plantations, it also was generally the most frequent.

T. aculeatum competes with *O. longinoda* as the most frequent in cocoa trees, as well as in trees of the secondary forest while being challenged at the forest edge by *C. striatula* and *Pheidole megacephala*. In the canopy of the mature forest of south Cameroon, it was never found in tree foliage, but it was on lianas.

C. striatula which was frequent in low formations (cocoa trees and forest edge) was absent in the two forest canopies, probably because of nesting preferences.

Therefore, a range of specialization between these 5 dominant species becomes apparent although flexibility in the choice of nesting trees was observed. The density of other dominant species is too low to draw conclusions.

Relationships Between Dominant and Nondominant Ant Species.

In the forest, each tree sheltered nondominant ant species in the canopy (Table 4). On the two trees not previously cited as sheltering dominant or subdominant ants we found: *Platythyrea conradti*, *Anochetus* sp. (two Ponerinae; non-populous societies) and *Camponotus* sp. 2 under epiphyte ferns and in rotten hollowed branches of the giant *Microberlinia bisulcata* (Fig 1: n° 10), and *Pheidole* sp. A (very discrete) on the *Lannea welwitschii* (Fig. 1: n° 41).

In other cases, nondominant ants are associated with subdominantor dominant species. Two of the latter, *A. mocquerisi* and *C. depressa*, tolerated a high rate of nondominant species while two others, *T. aculeatum* and *O. longinoda*, tolerated few nondominant species in their territory.

At the forest edge, both of the latter species and *C. striatula* tolerated

Table 4. Relationships between dominant and nondominant ant species at the level of the canopy of the old secondary rain forest. The first series of numbers corresponds to numbers of trees occupied as territories by each dominant species. (*1): very large society with status apparently equivalent to a dominant; (*Ato*): *Atopomyrmex mocquerysi*; (*Crc*): *Crematogaster clariventris*; (*Crd*): *Crematogaster depressa*; (*Phe*): *Pheidole megacephala*; (*Ta*): *Tetramorium aculeatum*; (*Oe*): *Oecophylla longinoda*.

NON-DOMINANT ANT SPECIES	WITHOUT DOMINANT 4	DOMINANT ANT SPECIES Ato 3	Crc 3	Crd 12	Phe 1	Tac 8	Oe 10	TOTAL 41
PONERINAE								
Anochetus sp.	1	2	.	1	.	.	.	4
Platythyrea conradti	1	1	.	1	.	.	.	3
PSEUDOMYRMECINAE								
Tetraponera anthracina	*1	1	1	1	1	3	.	8
MYRMICINAE								
Cataulachus guineensis	.	1	.	6	1	.	.	8
Cataulachus lobata	.	1	.	4	.	.	1	6
Pheidole sp.A	1	.	.	1	.	.	1	3
FORMICINAE								
Camponotus brutus	.	.	1	2	1	.	.	4
Camponotus sp.1		.	.	2	.	.	.	2
Camponotus sp.2	1	1	1	2	.	.	1	6
Polyrhachis militaris	*1	1	.	7	.	1	.	10
TOTAL:	6	8	3	27	3	4	3	54
PERCENTAGES:	150	266.7	100	225	300	50	30	131.7

Statistical comparisons of percentages from contigency tables: *Oe/Tac*: χ^2_c=0.1<3.8;NS; *Oe/Ato*: χ^2_c=17.3>10.8; P<0.001; *Oe/Crd*: χ^2_c=16.3; P<0.001; *Tac/Ato*: χ^2_c=10.6>6.6; P<0.01; *Tac/Crd*: χ^2_c=12.1;P<0.001.

less nondominant ants than other dominant ants did (Table 3), as previously quoted by Room (1971), Taylor (1977), and Bigger (1981). The dominant species that most tolerated nondominant ones were *Pheidole megacephala*, *Myrmicaria opaciventris* and *C. acvapimensis*, three ground-nesting species. Only *P. megacephala* was found on the territories of other dominant species, this result been previously cited by Taylor (1977).

Some nondominant ants were tolerated on the territories of numerous dominant ants. Workers of *P. laboriosa* were observed at least once on the territory of each dominant species. A similar result is true for *Cataulachus* sp. and *Camponotus* sp.A, not seen on the territories of *C. acvapimensis* (only 3 plants with this ant), while *T. anthracina* is not tolerated by *O. longinoda* (we get a similar result in the forest; Table 4). *Cataulachus guineensis* and *Camponotus chrysurus* also were tolerated by numerous dominant ants.

The present results, summarized in Fig. 2, are not in conformity with those of Room (1971) and Taylor (1977) who worked in plantations and

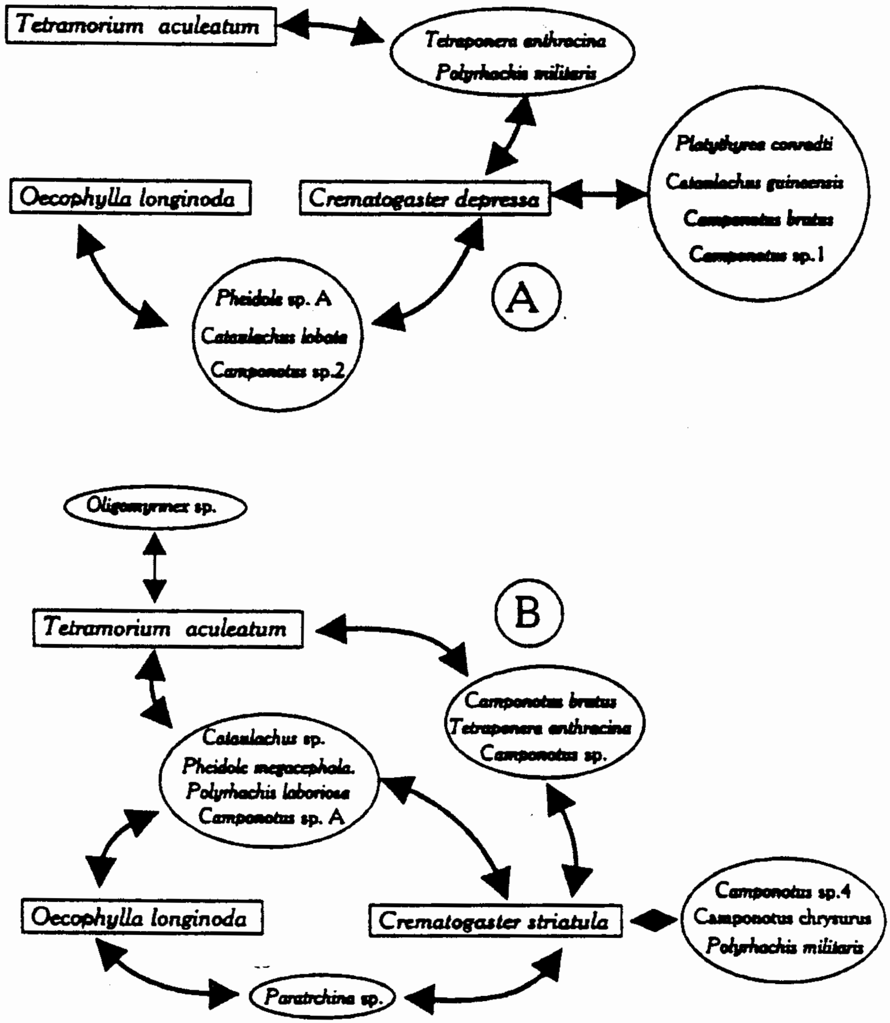

Fig.2: Associations between dominant and nondominant ant species. A: in the parcel of secondary forest where we considered only the three most frequent dominant species. B: at the forest edge where we considered the three least tolerant dominant species vis-a-vis nondominants. Large letters: dominant species; small letters: nondominant species.

concluded that to each dominant species corresponds certain nondominant species. These differences probably depend on distinct ecological situations. For instance, in our results *C. depressa* installed in wide territories of the forest canopy tolerated numerous nondominant species while this was not the case in the cocoa trees conquered as territories around the shade trees where it nested in Ghana. Also, the case of the forest edge (characterized by non-adjacent territories of dominant ants and numerous dominant ants «tolerant» vis-a-vis nondominant ants) is very different from that of cocoa tree plantations where the territories of non-tolerant, dominant ants are adjacent.

Although the areas of the two formations studied were of almost the same size and the plant diversity was superior in the forest, the ant diversity was richest at the forest edge. For nondominant ants, we found a species ratio of 10:20, and 54:165 for societies. This difference is probably the consequence of the distribution of the dominant ant territories which are not adjacent at the forest edge, a situation permitting nondominant ants to reproduce and develop easily. When the societies reach a large size, some of them turn «dominant-like» and correspond to the subdominantstatus (see above).

CONCLUSIONS

In response to the 5 questions presented in the introduction, we can conclude:

1. The secondary forest and the forest edge (comparable to the pioneer stage of the reconstitution of the forest) are not occupied by the same dominant ant species, although certain species were found in the 2 formations (*P. megacephala*, *T. aculeatum*, and *O. longinoda*).

2. *C. depressa* was the only species occupying forest trees left during clearing, while trees that grew after clearing were occupied by different dominant ants, including *C. depressa*.

3. The correlation between certain ant species and certain tree species was impossible to establish but the ants do not occupy trees at random (see above).

4. We were unable to establish distinct communities of nondominant ants associated with dominants, but cetain dominant ant species tolerated nondominant ants more than others.

5. The 2 perturbed habitats studied favor the installation of subdominant ants, particularly at the forest edge where territories of true dominant ants are not adjacent, permitting subdominant societies to develop and to gain territories.

The present results thus contribute to a better knowledge of the status of dominant and subdominant ants.

Dominant ants are characterized by very populous societies able to construct their own nests from carton, tied leaves, or they are carpenters. They have strong intraspecific agressivity and do not tolerate each other except in rare cases where codominant species were observed. Two groups can be separated: *O. longinoda* and, to a lesser degree, *T.*

aculeatum tolerated only a few nondominant ants on their territories. While different *Crematogaster* and *A. mocquerisi* accept numerous nondominant ants on their territories.

Crematogaster striatula, also tolerated only a few nondominant ants on its territories, but it doesn't build carton nests. Consequently it is limited to nesting close to the ground.

Pheidole megacephala is a polygynic tramp species which is primarily ground-nesting, but is also able to nest in dead branches and damaged cocoa pods (Majer 1976a), and in the crevices of the bark of numerous forest trees (Ngnegueu & Dejean 1992; present results). It is considered as a dominant ant in Nigerian cocoa plantations where it can coexist with *O. longinoda* (Taylor 1977). On the contrary, it competes with *O. smaragdina* which it displaced in the coconut plantations of Solomon Islands (Greenslade 1971). The present results show that this species was tolerated on the territories of different dominant ants, and tolerated in its turn numerous nondominant ants on its territories.

Among subdominant ants, we have to distinguish terrestrial-nesting species such as *C. acvapimensis*, able to have territories in low vegetation formations (Majer 1972), from arboreal-nesting species. Among the latter, only certain societies can reach a population size large enough to control a territory, generally one tree crown. *T. anthracina*, *Cataulachus guineensis* and *Camponotus brutus* are limited to hollowed twigs and dead branches, and the cavities situated between epiphytes and the bark of the supporting tree. They were tolerated by numerous dominant ants and tolerant to nondominants, although they were agressive at the intraspecific level. *P. laboriosa* is also tolerated on the territories of dominant ants and agressive at the intraspecific level, but workers are able to construct their own nests, polydomous societies and are non tolerant to nondominant ants on the trees occupied by the societies (Table 3).

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