Structure et dynamique d'une communauté de termites à nids arboricoles en cocoteraie néo-guinéenne

Maurice LEPONCE

Thèse présentée en vue de l'obtention du grade de
Docteur en Sciences Agronomiques
Promoteur: Prof. J.M. PASTEELS, co-promoteur: Dr. Y. ROISIN.

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ORIGINE DES SOCIETES D'INSECTES. - Il est assez difficile de concevoir comment ont pu se former ces vastes communautés d'insectes qui donnent l'impression d'une organisation collective. Pour certains naturalistes, le facteur essentiel du groupement et de la cohésion serait l'attraction de l'individu par l'individu. D'autres mettent à la base du phénomène social l'attraction exercée par le lieu de naissance. D'autres encore soulignent l'importance des échanges sensuels entre les Insectes associés. Ceux-ci seraient liés l'un à l'autre par la gourmandise, soit de la bouche ou de l'odorat; la volupté réciproque serait le ciment social.

Jean Rostand (1936). Insectes.
Ed. Flammarion, p.57.

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1. Introduction générale

Structure et dynamique des communautés de termites

En règle générale, la richesse en espèces dans les communautés de termites tend à diminuer à mesure que l'on s'écarte de l'équateur (Wood & Sands 1978): la répartition des termites est en effet fortement conditionnée par la température (Emerson 1955) et la pluviométrie (Lepage 1983). A l'échelle locale, la structure et la dynamique des communautés de termites sont influencées par des variations du climat, de l'habitat (sol et végétation) et par l'interaction avec les autres espèces de la biocénose. Nous ne considérerons pas ici l'action des parasites et pathogènes en raison du manque de données concernant leur impact au niveau des communautés.

Climat, végétation et sol

Les aléas climatiques peuvent avoir de profondes répercussions sur les populations de termites. En savane, les populations de termites fourrageurs peuvent fortement diminuer après de fortes sécheresses en raison de la diminution de nourriture disponible mais se rétablissent rapidement dès la réapparition des pluies (Watson & Gay 1970, Pomeroy 1983). Les conséquences du feu sont similaires à celles de la sécheresse (Benzie 1986). Les caractéristiques du sol ont un impact direct sur la disponibilité en eau, en sites de nidification et sur la végétation et peuvent affecter fortement la distribution des espèces souterraines et humivores (Bodot 1967). La végétation affecte la distribution des espèces. Ainsi *Trinervitermes oeconomus* et *T. occidentalis* s'observent sous le couvert de la végétation ligneuse alors que *T. geminatus* est dominante dans les zones ouvertes. Cette répartition serait, selon Sands (1965), liée à l'absence de stockage de nourriture chez les deux premières espèces qui ne pourraient pas, contrairement à *T. geminatus* — qui elle stocke —, survivre à la pénurie de nourriture en saison sèche dans les zones ouvertes. Dans les zones particulièrement exposées au soleil et au vent, la thermorégulation des nids est généralement rendue possible par l'adoption d'une architecture massive avec des nids aux parois épaisses (e.g. *Macrotermes*: Lüscher 1961). D'autres termites, parmi lesquels certains *Amitermes* (Gay & Calaby 1970, Grigg 1973, Grigg & Underwood 1977, Jacklyn 1991), *Drepanotermes* *perniger* (Watson & Perry 1981), *Tumulitermes hastilis* (Hill 1942), ... ont adopté une tout autre stratégie et orientent leur nid. Ce phénomène a été le mieux étudié chez *Amitermes meridionalis* qui construit des nids aplatis orientés de telle façon que, en saison sèche, lorsque la température nocturne peut descendre jusqu'à 5°C, la face Est du nid soit réchauffée rapidement le matin et atteigne un plateau à environ 25°C jusqu'au coucher du soleil (Jacklyn 1992).

Compétition entre termites

La compétition intra- et interspécifique peut être mise en évidence de manière directe, ainsi que leur importance relative mesurée, en manipulant expérimentalement la densité des colonies et en mesurant les réponses en terme de densité, de croissance, de mortalité des colonies, ... qui s'ensuivent (Connell 1983, Schoener 1983). Ce type d'expérience n'a jamais été réalisé à notre connaissance chez les termites, probablement en raison des difficultés de manipulation et de contrôle. L'ajout de colonies dans une communauté est en effet quasi exclu car la transplantation est souvent perturbante pour des termites à nid arboricole ou impossible pour des colonies à nid partiellement ou totalement souterrain. Par contre, l'enlèvement de colonies serait réalisable dans le cas des termites. Les quelques cas d'évidence directe de compétition disponibles dans la littérature concernent des observations de batailles intercoloniales naturelles ou provoquées (Levings & Adams 1984, Darlington 1982b, Jones 1993). Pour le reste, la compétition entre colonies de termites a toujours été suggérée de manière indirecte en analysant la distribution spatiale des colonies, la relation entre la distance et taille des colonies voisines, le taux de survie des jeunes colonies dans le milieu, la distribution des endroits où les nouvelles colonies croissent le plus vite, ... (par exemple, Pomeroy 1989).

Compétition intraspécifique

Agressivité intraspécifique

L'agressivité intraspécifique est généralisée chez les termites (Andrews 1911, Nel 1968, Clément 1978, 1980, Howick & Creffield 1980, Darlington 1982a & b, Thorne 1982a, Levings & Adams 1984, Abe & Darlington 1985, Traniello & Beshers 1985, Roisin *et al.* 1987, Binder 1988, Su & Scheffrahn 1988, Pearce *et al.* 1990, Adams 1991, Thorne & Haverty 1991, Jones 1993, Kettler & Leuthold 1995). Quelques populations semblent cependant faire exception à cette règle: les *Coptotermes formosanus* de Floride (Su & Haverty 1991) et de Louisiane (Delaplane 1991), les *Reticulitermes santonensis* français

(Clément 1986) ... Dans le cas de *Coptotermes formosanus* cette absence d'antagonisme pourrait être liée à une faible variabilité génétique de la population, probablement issue d'une introduction unique (Su & Haverty 1991).

Territorialité

Le territoire sera entendu ici comme une aire défendue contre des organismes ayant des niches écologiques proches (Baroni Urbani 1979). Chez les insectes sociaux, l'établissement et la maintenance du territoire sont basés sur une division du travail et sur un système complexe de communication (Hölldobler & Lumsden 1980). La plupart des recherches ont été concentrées sur les fourmis. Chez les fourmis, les stratégies territoriales sont associées à la distribution dans l'espace et dans le temps des ressources qu'elles exploitent. Lorsque les ressources sont stables, à la fois dans l'espace et dans le temps, on rencontre une stratégie de territoire absolu (*absolute territory*) typique de *Oecophylla longinoda* dont les ouvrières patrouillent continuellement à partir d'un réseau de nids décentralisés (Fig. 1A). Lorsque les ressources se renouvellent continuellement mais sont irrégulièrement distribuées dans l'espace on observe des pistes permanentes (*trunk-trail territories*) typiques de *Pogonomyrmex* spp. dont les ouvières empruntent un réseau bien établi de pistes à partir desquelles elles divergent et partent en excursion à la recherche de graines (Hölldobler 1976, Fig. 1B). Des territoires spatio-temporels (*spatio-temporal territories*) où seuls certains secteurs de l'aire de récolte sont défendus à un moment donné sont adoptés par des espèces telles *Myrmecocystus* spp. qui exploite des ressources variant à la fois dans l'espace et dans le temps, des termites par exemple (Fig. 1C).

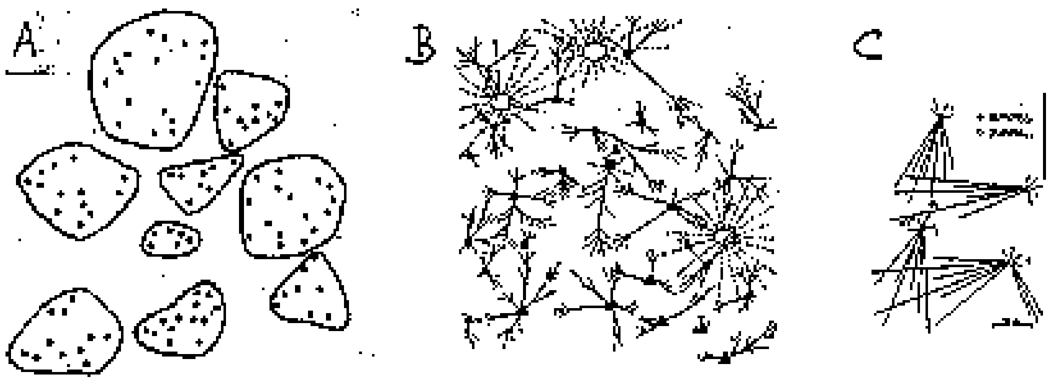

Figure 1: Trois grands types de stratégies territoriales chez les fourmis: A: territoires absolus d'*Oecophylla longinoda*: les arbres occupés par cette espèce sont indiqués par des cercles. Le territoire occupé par chaque colonie est entouré d'une ligne (d'après Hölldobler 1979), B: pistes permanentes de *Pogonomyrmex maricopa* (ellipses), *P. rugosus* (carrés) et *P. barbatus* (triangles) (d'après Hölldobler 1976 modifié), C: directions des pistes de *Myrmecocystus mimicus* et *M. depilis* (d'après Hölldobler 1981). Les trois schémas sont à la même échelle (5 mm = 10 m)

Chez les termites on doit s'attendre à des stratégies moins diversifiées parce que leur régime alimentaire est uniforme, toujours à base de cellulose. Comme pour les fourmis, on peut distinguer une gradation dans la défense: (1) défense du "nid" (pris au sens large, espace dans lequel la colonie est localisée sans qu'il s'agisse obligatoirement d'une construction); (2) défense du nid et des ressources de nourriture en cours d'exploitation; (3) défense du nid et d'une aire de récolte, ce qui peut être considéré comme la territorialité absolue. Dans la première catégorie on peut ranger les espèces qui ne construisent pas de nid proprement dit et qui se contentent de miner le bois (Kalotermitidae et Termopsidae): leur "territoire" se limite à la zone de bois exploitée. Les deux autres catégories regroupent les termites qui construisent des nids et un réseau de galeries dont une partie mène aux sources de nourriture. Ces nids ne sont pas forcément centralisés mais constituent parfois un système diffus (Pearce *et al.* 1990). La majorité des espèces de termites sont sans doute à ranger dans la deuxième catégorie. Les termites dont les moeurs s'apparentent le plus aux fourmis sont ceux qui partent en excursion à ciel ouvert et moissonnent des lichens. Ainsi la stratégie territoriale de *Longipeditermes longipes* dont les pistes changent continuellement (Gray & Dhanarajan 1974) peut être comparée à un territoire spatio-temporel. Par contre, *Hospitalitermes monoceros*, espèce au régime alimentaire similaire, emprunte des pistes persistant des semaines voire des mois (Petch 1913 *in* Gray & Dhanarajan 1974) et s'apparente donc plus aux pistes permanentes de fourmis. L'analogie avec les pistes permanentes est aussi la plus appropriée pour les termites qui vivent confinés dans leurs galeries et explorent peu le reste de l'environnement. Ces réseaux de pistes, très difficiles à suivre dans ou sur le sol ne sont bien connus que chez quelques espèces. Les réseaux de *Coptotermes acinaciformis* se prolongent jusqu'à 50 m du nid et les galeries sont abandonnées une fois que la source de nourriture auxquelles elles menaient est épuisée (Fig. 2A) (Greaves 1962). *Hodotermes mossambicus*, un termite qui explore individuellement puis moissonne en groupe au départ de trous dans le sol (Heidecker & Leuthold 1984), occupe des territoires définis (Nel 1968) mais dont le mode de défense n'est pas connu. *Macrotermes michaelseni* construit un réseau de galeries souterraines qui peut s'étendre jusqu'à 50 m du nid et qui donne accès, par des trous, aux débris végétaux en surface (Fig. 2B) (Darlington 1982b). Ce réseau semble permanent et sa longueur totale a été estimée à 6 km pour une seule colonie. *M. michaelseni* n'utilise qu'une partie de ce réseau à la fois mais alterne périodiquement les zones de récolte (Lepage 1981a, 1983). L'aire de récolte est effectivement défendue puisque Darlington a découvert des cadavres témoignant de batailles à la frontière de deux territoires. Cependant, les zones temporairement désertées restent sans défense. De jeunes colonies sont parfois présentes au sein du territoire d'une colonie mature mais se trouvent, dans leurs premiers stades tout au moins, plus en profondeur (en deçà de 20 cm) que les galeries de la colonie mature (5-15 cm sous la surface du sol) (Abe & Darlington 1985). Cependant, lorsque par la suite les galeries de la jeune colonie rejoignent le niveau exploré par la colonie mature, les chances de survie de la jeune colonie semblent très faibles. Ce processus expliquerait la dispersion régulière des nids et la très faible proportion de jeunes colonies dans le milieu (Darlington 1982a). Dans les mangroves de Panama, Levings & Adams (1984) ont cartographié le réseau de galeries couvertes — rendu obligatoirement arboricole par les inondations — de *Nasutitermes nigriceps* et *N. corniger* (Fig. 2C). Des batailles naturelles entre colonies voisines de *N. nigriceps* se rencontrant à une source de nourriture ont pu être observées et se sont terminées dans les 24 h par le retrait d'une colonie laissant une lacune entre les deux territoires. Ces “no-termites' land” séparaient en fait chacune des colonies de *Nasutitermes* sp. rappelant la répartition des territoires de fourmis dominantes en mosaïque (*ant mosaic*) (Majer 1993, Adams 1994a, b). Chez *Heterotermes aureus,* termite à nid hypogé vivant dans le désert du Sonora (Arizona), des conflits territoriaux entre colonies ont été mis en évidence grâce au quadrillage du sol par un réseau d'appâts (Jones 1993, Haverty *et al.* 1975). Les frontières des territoires d'*H. aureus* changent peu au cours du temps et sont séparées par des “no-termites' land” (Fig. 3).

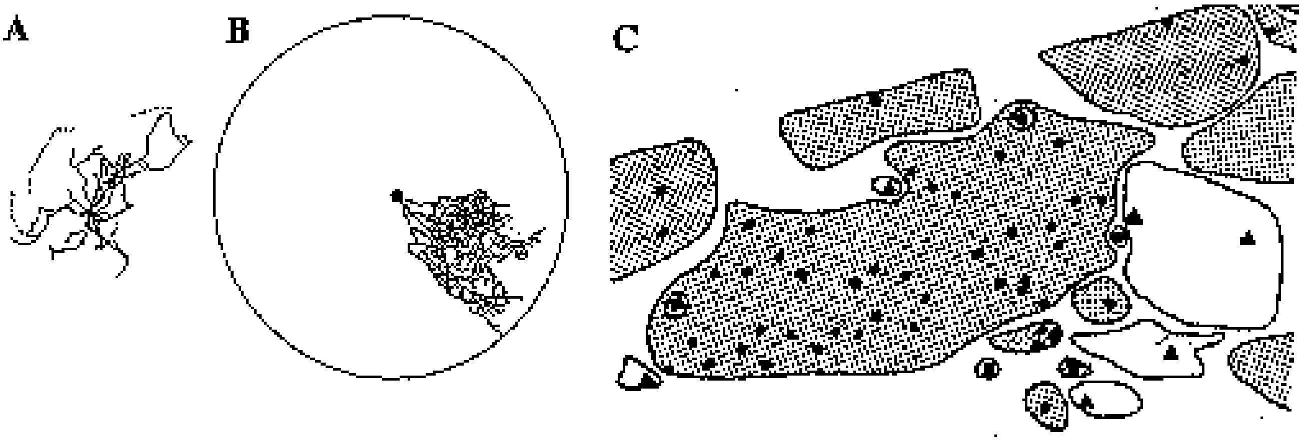

Figure 2: Différentes formes de territorialité chez les termites. Le territoire est délimité par une ligne continue (occupation à un moment donné) ou discontinue (occupation antérieure). A: réseau de galeries de *Coptotermes acinaciformis* (d'après Greaves 1962); B: territoire approximativement circulaire de *Macrotermes michaelseni* avec, dans un secteur, le détail du réseau de galeries souterraines permanentes (d'après Darlington 1982b); C: territoires exclusivement arboricoles de 11 colonies de *N. corniger* (nids indiqués par des cercles noirs) et de 6 colonies de *N. nigriceps* (nids indiqués par des triangles noirs) dans une mangrove à Panama. Des souches occupées par *Termes panamaensis* sont indiquées par un carré noir (d'après Levings & Adams 1984). Les trois schémas sont à la même échelle (5 mm = 10 m).

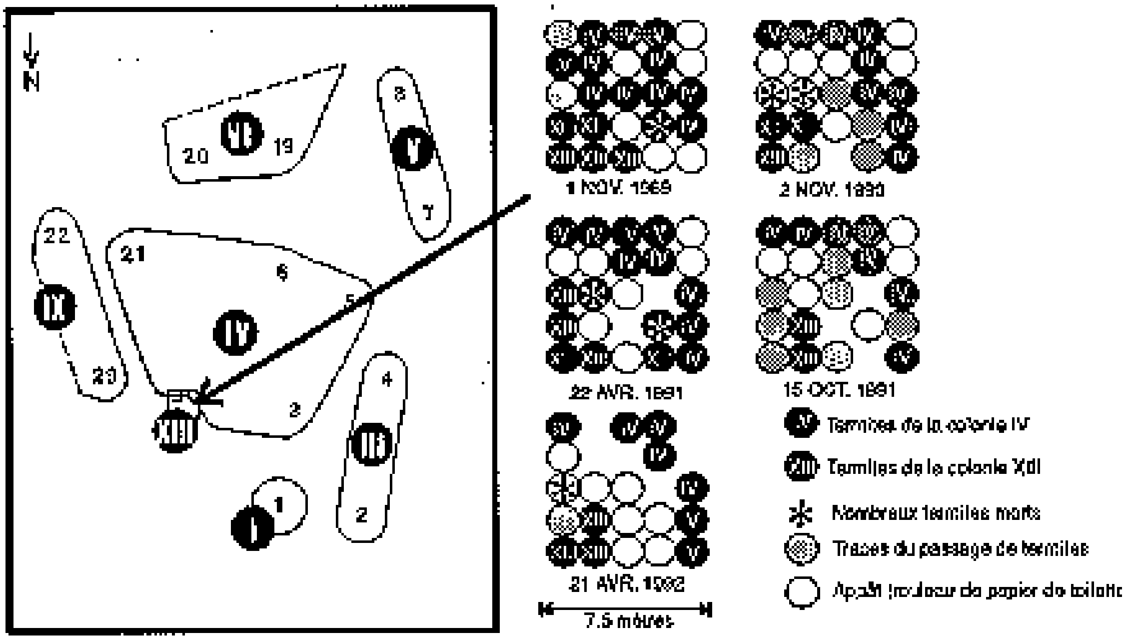

Figure 3: Territoires de 7 colonies d'*Heterotermes aureus* délimités au moyen d'appâts et détail des frontières des territoires entre les colonies XIII et IV à intervalles de 6 à 12 mois (d'après Jones 1993, modifié).

Les batailles territoriales sont coûteuses et des mécanismes comme la divergence des pistes après batailles (Thorne 1982a, Levings & Adams 1984) ou la construction de séparations en terre (Pearce *et al.* 1990) semblent être des mécanismes pour éviter que les confrontations ne soient trop fréquentes. Le territoire doit être défendable et doit rapporter plus d'énergie qu'il n'en coûte (Hölldobler & Lumsden 1980); sa taille est donc limitée. Chez les fourmis de feu (*Solenopsis invicta*), dont les territoires s'organisent en une mosaïque, il a été démontré que la forme et la taille du territoire de chaque colonie pouvaient être prédites à partir de 3 paramètres: l'importance de la colonie en termes de population, l'éloignement de la frontière du territoire par rapport au nid et une contrainte de compression du territoire due à la présence de colonies voisines (Adams 1994b). Chez les termites, dont la territorialité a été moins étudiée que chez les fourmis, une bonne corrélation entre la taille du nid et celle du territoire a été démontrée dans certains cas (Banerjee 1975, Adams & Levings 1987). Une augmentation de la nourriture disponible peut entraîner une réduction de la taille des territoires et permettre l'implantation de nouvelles colonies (Collins 1982). Inversement, en cas de compétition pour la nourriture, une colonie pourrait s'approprier le réseau de galeries d'une colonie voisine (Greaves 1962). De nouvelles colonies peuvent s'établir dans le milieu tant que les colonies existantes ne se partagent pas l'ensemble de l'espace disponible.

Ségrégation spatiale des colonies de même espèce

Une dispersion régulière des colonies (*overdispersion*), qui correspond à un arrangement spatial où les colonies tendent à maximiser la distance qui les sépare de leurs voisins, peut indiquer des phénomènes de compétition intraspécifique. La dispersion régulière résulte de la maintenance d'un territoire par chaque colonie de termite. L'échelle du motif dépend de l'espèce de termite et de la quantité de nourriture disponible dans l'écosystème (Darlington 1985a). La distribution des nids, agrégée, aléatoire ou régulière est généralement mesurée par la méthode de Clark & Evans (1954) (tableau 1). Le coefficient de dispersion ***a*** calculé par la méthode de Clark & Evans varie de 0, lorsque toutes les colonies sont agrégées en un point, à 1.158 si toutes les colonies sont disposées régulièrement en triangles équilatéraux, en passant par 0.25 qui correspond à une distribution aléatoire. Les valeurs inférieures à 0.25 indiquent donc l'agrégation tandis que celles supérieures à 0.25 indiquent une distribution régulière des colonies. Les résultats de cette méthode sont influencés par l'échelle à laquelle on travaille (Spain *et al.* 1986) et par l'uniformité de l'habitat. Un traitement correct des données implique aussi que l'on connaisse la distribution spatiale des colonies polycaliques (Holt & Easey 1985). Le tableau 1 montre que les nids de même espèce sont distribués régulièrement dans plus de la moitié des cas. La dispersion peut varier en fonction de l'habitat; ainsi Wood & Lee (1971) observent, entre la forêt basse et la savane arborée, une augmentation du coefficient de dispersion des nids d'*Amitermes vitiosus* (tableau 1) qu'ils interprètent comme un signe d'accroissement de la compétition pour les sites de nidification, dû à l'hétérogénéité du sol en savane. Une distribution aléatoire ou une tendance à la distribution aléatoire ont été rencontrées dans 6 cas sur 13 (tableau 1, cas A1-A13). Quant aux colonies de *Macrotermes bellicosus*, elles ne sont pas distribuées régulièrement d'après les données de Collins (1981) au Nigéria tandis que Lepage (1984) en Côte d'Ivoire observe, pour cette même espèce, une distribution aléatoire ou régulière selon le milieu. Pomeroy (1989) suggère que la forte prédation par les fourmis maintiendrait le nombre de *M. bellicosus* en dessous de la capacité portante du milieu et que donc la compétition intraspécifique ne se marquerait pas, expliquant les cas de distribution aléatoire observés par Collins et Lepage. Quant à l'agrégation des nids de *Trinervitermes geminatus*, elle a aussi été mise sur le compte de l'hétérogénéité de l'habitat, cette espèce se concentrant dans les endroits fortement ensoleillés (Sands 1965).

Tableau 1: Etudes sur la distribution spatiale des nids de termites d’une et de plusieurs espèces

	Population / Communauté	Habitat	Taille de la parcelle	Espacement des nids	Coefficient de dispersion ***a*** (Clark & Evans 1954) ou autre mesure de la distribution	Source et région
A.	**Population**					
1	*Trinervitermes geminatus*	savane arborée, savane herbeuse	0.04 ha x 10	-		Sands 1965, Nigéria, alt:700 m
2	*Macrotermes bellicosus*	savane arborée *(savanna woodland)*	6.00 ha	0	a = 0.37, 0.28, 0.22 pour un même site à 1 an d'intervalle	Collins 1981, Nigeria
3	*Macrotermes bellicosus*	plateau latéritique		0	a = 0.22	Lepage 1984, Côte d'Ivoire
4	*Macrotermes bellicosus*	forêt sèche		+	a = 0.49	Lepage 1984, Côte d'Ivoire
5	*Macrotermes bellicosus*	savane arborée *(forest savanna)*		+	a= 0.33 - 0.45 (2 sites)	Lepage 1984, Côte d'Ivoire
6	*Macrotermes bellicosus*	savane brousailleuse *(scrub savanna)*		0	a = 0.22	Lepage 1984, Côte d'Ivoire
7	*Amitermes vitiosus*	forêt basse *(low woodland)*	0.45 ha	+	a=0.51	Wood & Lee 1971, Nord de l'Australie
8	*Amitermes vitiosus*	savane arborée *(savanna woodland)*	0.48 ha	+	a = 0.68	Wood & Lee 1971, Nord de l'Australie
9	*Nasutitermes triodiae*	savane arbustive *(tree savanna)*		0, +	a = 0.22-0.34 selon le site (n=2 sites)	Wood & Lee 1971, Nord de l'Australie
10	*Amitermes laurensis*	savane arborée éclaircie *(savanna woodland cleared)*	0.28 - 1.71 ha	+	a = 0.38-0.55 selon le site (n= 5 sites)	Wood & Lee 1971, Nord de l'Australie
11	*Nasutitermes magnus*	prairie *(pasture)*	1.00 ha	+	a = 0.30	Wood & Lee 1971, Nord de l'Australie
12	*Nasutitermes exitiosus*	forêt sclérophylle sèche		0/-, +	a = 0.22-0.45 selon le site (n=3 sites)	Wood & Lee 1971, Nord de l'Australie
13	*Amitermes laurensis*	forêt éclaircie (*open grassy woodland, all trees poisoned*)	1.00 ha	0	a= 0.29	Holt & Greenslade 1979, Australie
B.	**Communauté**					
1	*Coptotermes lacteus, Nasutitermes exitiosus*	forêt sclérophylle sèche	13.20 ha	+	a = 0.63	Wood & Lee 1971, Nord de l'Australie
2	*Tumulitermes hastilis, A. vitiosus, Drepanotermes spp.*	savane arborée *(savanna woodland)*	0.59 ha	+	a = 0.86	Wood & Lee 1971, Nord de l'Australie
3	*Macrotermes subhyalinus, Macrotermes michaelseni*	savane herbeuse	0.93 ha	+	indice d'agrégation R= 1.396 (Clark & Evans 1954)	Pomeroy 1989, Kenya, 1100 m
4	*Amitermes laurensis, Tumulitermes pastinator, Drepanotermes rubriceps*	forêt claire *(open woodland)*	1.0 ha	+ , 0 selon parcelle	Empirical Distribution Function G & F	Spain, Sinclair & Diggle 1986, Pointe N. de l'Australie
5	*A. laurensis, T. pastinator, D. rubriceps*	forêt claire *(open woodland)*	1.0 ha	-	id	Spain, Sinclair & Diggle 1986, Pointe N. de l'Australie
6	*A. vitiosus, T. pastinator, Nasutitermes magnus, Drepanotermes spp.*	forêt claire *(open woodland, grey soil)*	0.3 -0.5 ha	+ , 0 selon parcelle	id	Spain, Sinclair & Diggle 1986, Pointe N. de l'Australie
7	*id*	forêt claire *(open woodland, red soil)*	0.5 ha	+	id	Spain, Sinclair & Diggle 1986, Pointe N. de l'Australie
8	*id*	forêt claire *(open woodland,yellow soil)*	0.5 ha	+	id	Spain, Sinclair & Diggle 1986, Pointe N. de l'Australie
9	*Amitermes laurensis, A. scopulus, Nasutitermes triodiae*	savane herbeuse *(grasses and sparse trees)*	2.0 - 2.5 ha	+	id	Spain, Sinclair & Diggle 1986, Pointe N. de l'Australie
10	*Reticulitermes spp.*	forêt de pin *(pine forest)*	1.0 ha	-	a = 0.14 - 0.22	Howard et al. 1982, Mississippi

Indépendamment de la régularité de la distribution, le fait que la distance entre les nids était proportionnelle à la taille des nids chez *Macrotermes bellicosus* (Lepage 1984), *M. subhyalinus*, *M. michaelseni* (Pomeroy 1989) et *Nasutitermes exitiosus* (Wood & Lee 1971), plaide pour l'hypothèse d'une compétition intraspécifique chez ces espèces.

Compétition interspécifique

Agressivité interspécifique

L'agressivité interspécifique semble généralisée (Greaves 1962, Ikehara 1966, Bodot 1967, Nel 1968, Clément 1978, 1980, Springhetti & Amorelli 1982, Thorne 1982a, Levings & Adams 1984, Traniello & Beshers 1985, Chambers & Zungoli 1988, Su & Scheffrahn 1988, Haverty & Thorne 1989, Bagnères *et al.* 1991, Jones & Trosset 1991, Thorne & Haverty 1991, Kettler & Leuthold 1995). Lorsque des termites d'espèces différentes entrent en contact, sur une aire de récolte de nourriture ou à une source de nourriture, on peut donc s'attendre à des combats. Les capacités défensives des soldats diffèrent selon les espèces (Deligne 1971, Deligne *et al.* 1981). Le nombre de défenseurs (Jones & Trosset 1991), leur agilité (Badawi *et al.* 1984), leur taille, ... peuvent avantager une espèce par rapport à une autre. Une hiérarchie des capacités défensives entre espèces sympatriques peut être élaborée à partir de confrontations de lots d'individus en laboratoire (Ikehara 1966) mais n'est pas forcément représentative des capacités compétitives en nature où entrent en jeu des facteurs tels la structure du nid (Deligne & Pasteels 1982), la rapidité du recrutement qui peut compenser une infériorité numérique initiale, la distance par rapport au nid (ou la calie la plus proche chez les espèces polycaliques) ... (Adams 1990).

Manifestations de compétition interspécifique

Ségrégation des espèces

Des phénomènes de compétition interspécifique peuvent être suggérés par une ségrégation des espèces. Josens (1972) remarque que des bûchettes disposées dans le sol selon une trame régulière, sont beaucoup plus rarement attaquées simultanément par *Ancistrotermes cavithorax* et *Microtermes toumodiensis* que si les espèces ne s'excluaient pas. Lorsque trouvées à la même bûchette, les 2 espèces étaient séparées par une cloison de terre. Calaby & Gay (1959) remarquent que les espèces de *Coptotermes* sympatriques ne sont jamais trouvées dans une même souche.

Dispersion régulière des colonies d'espèces différentes

Dans 6 parmi 9 communautés d'Afrique et d'Australie, les nids partiellement épigés étaient dispersés régulièrement (tableau 1). Wood & Lee (1971) observent que *Coptotermes lacteus* et *Nasutitermes exitiosus* ont tendance à maximiser leurs distances réciproques et à se répartir selon un maillage hexagonal et que les colonies de *N. exitiosus*, très populeuses, maintiennent les plus larges territoires. Ces mêmes auteurs, sur la base des données de la communauté composée de *Tumulitermes hastilis*, *Amitermes vitiosus* et *Drepanotermes* spp., remarquent une tendance à l'agrégation entre nids de même espèce qui pourrait indiquer que la compétition interspécifique est plus forte que la compétition intraspécifique; alternativement, les agrégations pourraient être dues à l'hétérogénéité de l'habitat. Dans deux autres communautés, les nids étaient, selon la taille de la parcelle, soit distribués aléatoirement soit dispersés régulièrement (Spain *et al.* 1986, tableau 1: B4 et B6). Enfin les nids étaient agrégés dans une autre communauté, peut-être suite à l'hétérogénéité du sol et ou à l'organisation polycalique de certaines colonies (Spain *et al.* 1986, tableau 1: B5). Les colonies à nids souterrains de *Reticulitermes flavipes* et *R. virginicus*, repérées dans les souches d'une forêt de pin (*Pinus palustris*), étaient agrégées vraisemblablement suite à l'hétérogénéité de l'habitat: la première espèce préférant le haut et la seconde le bas des collines, plus humide (Howard *et al.* 1982, tableau 1: B10). D'une manière générale on peut donc conclure que la dispersion régulière des nids d'espèces aux besoins similaires est fréquente.

Territorialité et déplacement compétitif

Dans les mangroves de Panama, une ségrégation horizontale des territoires des colonies de *Nasutitermes* arboricoles s'opère à la fois intraspécifiquement et interspécifiquement (Fig. 2C, Levings & Adams 1984, Adams & Levings 1987). En connectant artificiellement des territoires adjacents, Levings & Adams ont observé soit des batailles suivies d'une divergence des galeries des 2 colonies soit l'élimination rapide d'une petite colonie de *N. nigriceps* par une colonie de *N. corniger*.

Des combats interspécifiques dans les zones de contact entre *Heterotermes aureus* et *Gnathamitermes perplexus* ont été révélés au sein de parcelles quadrillées d'appâts (dispositif expérimental similaire à celui présenté en Fig. 3 p. 6) par la présence conjointe de cadavres des deux espèces (Jones & Trosset 1991). *H. aureus*, bénéficiant d'un avantage numérique et d'un système de galeries bien développé, déplaçait agressivement *G. perplexus* des appâts. Les sites où avaient eu lieu un conflit étaient ensuite évités par *G. perplexus.* A la Nouvelle-Orléans, l'espèce introduite, *Coptotermes formosanus*, semble remplacer localement les

Reticulitermes spp. indigènes (LaFage *in* Su & Scheffrahn 1988). Appliquant le principe du déplacement compétitif, Salick & Tho (1984) suggèrent que les *Coptotermes* spp. nuisibles pourraient être déplacées compétitivement par deux genres non-nuisibles *Odontotermes* spp. et *Schedorhinotermes* spp. dans les plantations de pins et de caoutchouc en Malaisie.

Envahissement de nids

L'occupation des nids d'une espèce par une ou plusieurs autres espèces de termites est un phénomène répandu. Les nids de *Macrotermes*, *Cubitermes*, *Bellicositermes*, *Procubitermes*, *Apilitermes*, *Trinervitermes* en Afrique (Grassé 1944, 1986, Ernst 1960, Bodot 1964, Bouillon & Mathot 1965, Sands 1965, Bouillon 1970, Collins 1980, Ferrard 1982), les nids de *Syntermes*, *Cornitermes* et *Constrictotermes* en Amérique du Sud (Emerson 1938, 1955, Araujo 1970, Mathews 1977), les nids d'*Hospitalitermes* en Asie du S.-E (John 1913 *in* Collins 1980) et les nids de *Coptotermes* en Australie (Hill 1942, Gay & Calaby 1970) contiennent des termites étrangers. Ernst (1960) observe par exemple que 70% des nids de *Cubitermes* contiennent d'autres espèces de termites. L'antagonisme est de règle en cas de contact, aussi les différentes espèces vivent-elles dans des zones séparées du nid. Dans certains cas les termites étrangers sont des inquilins obligatoires (Emerson 1938, 1955). Collins (1980) souligne que la cohabitation de plusieurs espèces s'observe souvent dans des nids quasi abandonnés par leur constructeur originel. Les relations exactes qu'entretiennent les occupants étrangers avec leurs hôtes sont mal connues: certaines espèces étrangères paraissent envahir progressivement le nid (Bodot 1964). Ainsi, *Amitermes evuncifer* envahit les nids vivants de *Cubitermes severus*, de *Trinervitermes trinervius* (Bodot 1967) et de *T. geminatus* (Josens 1972). Bodot relate que 80% des colonies d'*Amitermes* occupent secondairement des nids d'une autre espèce dont ils remanient progressivement l'architecture (Bodot 1967). Au moment de l'essaimage, les ailés d'*A. evuncifer* semblent attirés par les masses sombres au niveau du sol, dont les termitières épigées d'autres espèces, ce qui pourrait favoriser le phénomène d'envahissement secondaire (Josens 1972).

Prédation

Les termites sont des proies faciles et abondantes mais, hormis les ailés lors des essaimages et les fourrageurs à ciel ouvert, les termites vivent assez bien protégés dans leurs structures ou dans leur source de nourriture. Les périodes d'essaimage sont apparemment une réponse à la pression de prédation: elles sont soit décalées par rapport aux pics d'activité des principaux prédateurs, soit synchronisées de manière à saturer les prédateurs ou soit encore irrégulières et fragmentées de façon à minimiser la formation d'une image de recherche par les prédateurs (Nutting 1979). Les prédateurs de termites sont tant des vertébrés que des invertébrés (revue de Wood & Sands 1978, Deligne *et al.* 1981, Nutting & Jones 1990). Face à cette variété de prédateurs nous nous concentrerons ici que sur les principaux, à savoir les fourmis.

La classification de Wheeler (1936) distingue différents types de relations fourmis/termites: (i) les fourmis razzieuses[1] (*termitharpactic ants*, *termite-raiders*) qui attaquent les colonies de termites; (ii) les fourmis termitolestiques (*lestobiotic ants*, *thief-ants*) prédatrices du couvain ou des termites invalides à partir d'un nid au voisinage de la termitière; (iii) les fourmis inquilines (*inquiline ants*) qui habitent la termitière et sont des prédateurs occasionnels de termites. Wheeler distingue 2 catégories supplémentaires: les fourmis cleptobiotiques (*footpad-ants*) qui dérobent les termites aux fourmis razzieuses et les fourmis qui vivent parmi les termites sans manifestation mutuelle d'hostilité (termitoxénie, *guest-ants*). Nous ne les retiendrons pas ici car la première correspond plutôt à une relation entre fourmis et la seconde peut se rattacher à l'inquilinisme.

Des fourmis "razzieuses" se retrouvent en Afrique (*Dorylus* spp. [Dorylinae]: Williams 1959, Bodot 1961, 1967, Lepage 1984, Darlington 1985b ; *Megaponera foetens* [Ponerinae]: Weber 1964, Longhurst *et al.* 1978, Longhurst & Howse 1979, Lepage 1981b), en Asie (*Leptogenys chinensis* [Ponerinae]: Maschwitz & Schönegge 1983), en Amérique du Sud (*Pachycondyla commutata* [Ponerinae]: Mill 1984), en Amérique Centrale (*Neivamyrmex nigrescens* [Ecitoninae]: Mirenda *et al.* 1980) ainsi qu'en Australie (*Iridomyrmex sanguineus* [Dolichoderinae]: Higashi & Ito 1989). Ces fourmis sont souvent des prédateurs spécialisés de termites et plus particulièrement de Macrotermitinae dans le cas des *Dorylus* spp., de *Megaponera foetens* et de *Leptogenys chinensis* (Wheeler 1936, Longhurst *et al.* 1978, Maschwitz & Schönegge 1983). Les raids de *M. foetens* sont déclenchés par une éclaireuse solitaire qui, après avoir localisé des termites, retourne au nid en déposant une piste chimique (Longhurst *et al.* 1978). De retour au nid, l'éclaireuse recrute un groupe d'ouvrières qui, guidées par la piste, capturent les termites en perçant les placards de sol que les termites construisent autour de leur source de nourriture. Les *M. foetens* détectent la présence de leur proie par l'odeur des termites imprégnée dans ces placards de sol. Les proies sont ensuite ramenées au nid en empruntant la piste en sens inverse. La tactique adoptée par *Leptogenys chinensis* est semblable à celle de *M. foetens* (Maschwitz & Schönegge 1983, Longhurst & Howse 1978). En Amérique Centrale les fourmis légionnaires *Neivamyrmex nigrescens*

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[1] la traduction des termes anglais a été empruntée à Grassé 1986

organisent des raids nocturnes capturant des fourmis et des petits groupes de termites (Mirenda *et al.* 1980). Les fourmis razzieuses ont généralement un impact marqué sur les populations de termites; ainsi en Afrique de l'Ouest (Bodot 1961, 1967, Lepage 1984) et de l'Est (Darlington 1985b) les raids de dorylines semblent être une importante, sinon la principale, source de mortalité des nids de *Macrotermes*; au Brésil, le prélèvement opéré par *Pachycondyla commutata* sur les populations de *Syntermes* spp. semble aussi très important (Mill 1984).

Les fourmis "termitolestiques" ou "lestobiotiques" sont généralement des Myrmicinae appartenant aux genres *Solenopsis*, *Monomorium* ou *Carebara* (Smythe & Coppel 1964, 1973). Il s'agit de fourmis de très petite taille qui nichent dans les nids de termites et se nourrissent généralement des oeufs ou des larves de leur hôte (Forel 1901 *in* Lepage & Darlington 1984). Les *Solenopsis molesta* construisent des séparations en terre pour s'isoler de leur hôte *Reticulitermes flavipes* (Smythe & Coppel 1964). La prédation par *Carebara vidua*, présente dans environ 2% des nids de *Macrotermes* spp., n'a jamais été observée en nature mais, si elle s'opère, il est probable que *C. vidua* se nourrit de termites adultes et non de larves (localisées dans des zones inexplorées par les fourmis) (Lepage & Darlington 1984). Les ouvriers de *Carebara* ne provoquent pas d'agression de la part de divers Macrotermitinae (Longhurst 1977 dans Lepage & Darlington 1984, Longhurst *et al.* 1979) à l'instar des ouvriers de *Solenopsis laeviceps* en contact avec leur hôte *Nasutitermes costalis* (Emerson *in* Wheeler 1936).

Les fourmis inquilines profitent généralement du nid de termites comme abri et source de nourriture en consommant des termites (morts ou vifs). L'inquilinisme des fourmis est exclusif chez certaines espèces telles les *Camponotus* spp. [Formicinae] trouvées dans les nids d'*Amitermes laurensis* (Higashi & Ito 1989) ou au contraire opportuniste; ainsi la proportion de nids de *Nasutitermes corniger* occupés par des fourmis varie de manière saisonnière avec des pics en saison des pluies et est plus importante dans les sites inondés (Jaffe *et al.* 1995). Dans certains cas, la présence de fourmis inquilines peut être bénéfique pour la colonie de termites. En Australie, les nids d'*Amitermes laurensis* semblent être efficacement prémunis contre les raids d'*Iridomyrmex sanguineus* grâce à la coopération dans la défense du nid des deux espèces de *Camponotus* inquilines (Higashi & Ito 1989). Outre la coopération pour la défense du nid, les termites peuvent bénéficier de la présence des fourmis inquilines en consommant les fourmis mortes et les autres déchets de la colonie de fourmis qui constituent un apport substantiel en azote pour les termites. Ainsi *Nasutitermes corniger* semble tolérer des fourmis inquilines dans ses nids, particulièrement celles, telle *Monacis bispinosa*, qui sont incapables de capturer des termites vivants (Jaffe *et al.* 1995). Jaffe *et al.* ont mis en évidence au moyen de traceurs radioactifs que *N. corniger* consommait effectivement des fourmis et/ou leurs déchets.

En réponse à la prédation des fourmis les termites ont développé des mécanismes de défense (Deligne *et al.* 1981, Kaib 1985). Le nid est un élément essentiel dans la défense contre les ennemis (Deligne *et al.* 1981). *Prohamitermes mirabilis* est capable d'obturer rapidement les orifices de communication entre les chambres de son nid par des boulettes préfabriquées (Tho & Maschwitz 1988) tandis que ces orifices sont obturés par la tête des soldats chez *Microcerotermes* (Deligne & Pasteels 1982). Les sécrétions défensives des soldats de termites sont des armes particulièrement efficaces contre les fourmis et ont, selon les espèces, des propriétés engluantes, toxiques ou phéromonales (Moore 1969, Quennedey & Deligne 1975, Prestwich 1979, Kaib 1982, Mill 1983). Ces trois propriétés sont cumulées chez certains Nasutitermitinae (Eisner *et al.* 1976, Vrkoc *et al.* 1978, Traniello 1981, Mill 1983, Roisin *et al.* 1990). Ceci expliquerait la répulsion de certaines fourmis telle *Iridomyrmex sanguineus* face à des *Nasutitermes* (Hill *in* Wheeler 1936).

Soulignons que la prédation n'est pas la seule interférence des fourmis vis-à-vis des termites; dans certains cas fourmis et termites peuvent entrer en compétition pour les sites de nidification; ainsi dans les forêts de basse altitude de Nouvelle-Guinée, tous les sites de nidification disponibles sont occupés soit par des fourmis soit par des termites (Wilson 1959). Enfin, dans les vergers de *Citrus*, la présence de nids arboricoles de *Nasutitermes costalis* est négativement corrélée avec la présence de nids d'*Azteca* sp. mais la nature de l'interférence n'est pas connue (Jutsum *et al.* 1981).

Coexistence d'espèces au sein d'une communauté

Bien que coexistant dans le même milieu, de nombreuses espèces ont des niches écologiques suffisamment différentes, de sorte qu'elles interfèrent peu. Les espèces peuvent différer quant à leur site de nidification, leur régime alimentaire, leur stratégie de récolte, leur stratégie de reproduction, leur rythme d'activité, leur espace de récolte, ...

Par ailleurs, nous avons déjà signalé certains mécanismes qui tendent à diminuer les combats interspécifiques: zones tampons entre territoires (Levings & Adams 1984) ou évitement de sites où des compétiteurs ont été rencontrés (Jones & Trosset 1991). Dans des confrontations en laboratoire, Nel (1968) note également que *Hodotermes mossambicus* et *Trinervitermes trinervoides* manifestent des comportements d'évitement plutôt que d'attaque. D'autres mécanismes, tel un effet répulsif de la phéromone de piste d'une espèce sur une autre, n'ont jamais été signalés. Au contraire, des *Trinervitermes bettonianus* ont été observés suivant la piste d'autres espèces de *Trinervitermes* (Oloo & McDowell 1982).

Objectif du travail

Lorsqu'on étudie l'organisation des communautés, on se heurte rapidement à la difficulté qui consiste à distinguer les effets de chacun des facteurs écologiques en éliminant quasi toutes les autres causes possibles. Un milieu artificiel telle une plantation, du fait de son homogénéité et du nombre limité d'espèces qu'elle accueille, permet de mieux distinguer les effets des différents facteurs. Les plantations de cocotiers en Nouvelle-Guinée présentaient certaines caractéristiques favorables à l'étude de l'organisation d'une communauté de termites:

1. le milieu était largement occupé par des termites à nids arboricoles dont les colonies étaient aisément repérables et mesurables.
2. un même arbre ne supportait apparemment jamais plus d'une espèce, ce qui suggère une exclusion mutuelle (Roisin *et al.* 1987).
3. des variations marquées dans l'abondance des termites s'observaient entre sites.
4. divers arrangements spatiaux des arbres ouvraient la possibilité d'évaluer l'influence de la densité des sites de nidification, de la densité de nourriture et du microclimat sur la communauté de termites.
5. l'arrangement régulier des arbres facilitait la cartographie des colonies de termites et un suivi dans le temps de la structure de la communauté.
6. des habitats de différents âges connus étaient présents.

De surcroît, une importante documentation sur la biologie des *Nasutitermes* vivant dans ce milieu était disponible grâce aux travaux de Roisin, Pasteels et Everaerts (Roisin & Pasteels 1985a, b; Roisin 1986, Roisin & Pasteels 1986a, b, c; Roisin 1987; Roisin & Pasteels 1987a, b; Roisin *et al.* 1987; Everaerts 1988; Everaerts *et al.* 1988a; Everaerts *et al.* 1988b; Pasteels *et al.* 1988; Everaerts *et al.* 1990; Roisin *et al.* 1990; Roisin & Pasteels *sous presse*).

Le but du présent travail était de déterminer comment s'organise localement une communauté de termites à nids arboricoles et en particulier d'identifier:

1. les principaux paramètres écologiques qui déterminent la distribution et l'abondance de ces termites;
2. les mécanismes qui permettent la coexistence de colonies antagonistes;

3. la territorialité de ces termites arboricoles —à titre de comparaison avec le travail de Levings & Adams (1984, cf. p. 5); dans le cas présent sans la contrainte d'un réseau de galeries exclusivement arboricoles—.

Sites d'étude

Les sites d'études sont localisés dans les plantations de cocotiers qui bordent la côte Nord-Est de la Nouvelle-Guinée (Fig. 4). La région la plus prospectée est celle de Hansa Bay, district de Bogia, province de Madang, près de la Station Biologique Léopold III, île de Laing (4°10'S et 144°52'E). Le climat est de type tropical humide avec une température relativement constante tout au long de l'année et comprise entre 22°C et 34°C (Gressitt 1982, Bouillon *et al.* 1986). La saison des pluies s'étend d'octobre à avril et la saison sèche de mai à septembre. Les données météorologiques mesurées à l'île de Laing et à Bogia figurent en annexe **4**.

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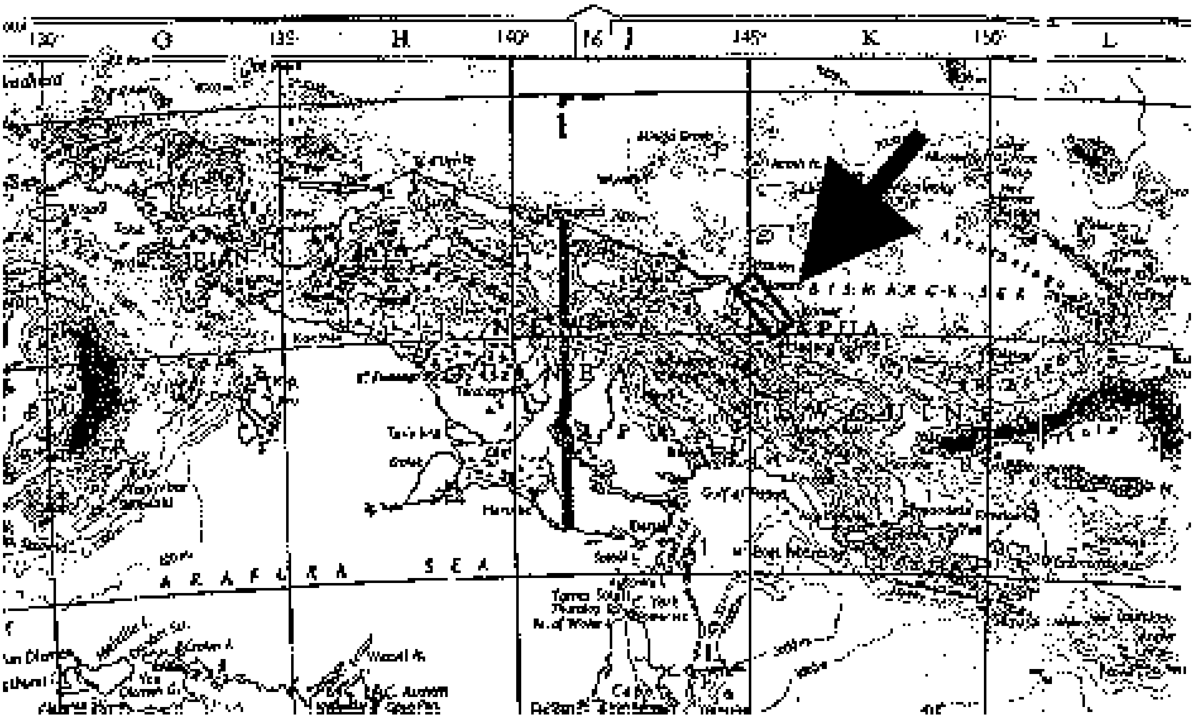

Figure 4: Carte de la Nouvelle-Guinée et des régions avoisinantes. La zone encadrée représente la zone côtière prospectée lors des recherches.

En Papouasie-Nouvelle-Guinée, les premières cocoteraies ont été plantées vers les années 1880 par les colons allemands en Nouvelle-Bretagne et ont été limitées aux îles jusqu'en 1907 (De Silva 1989). L'expansion des plantations sur la zone côtière se réalisa à partir de cette époque et les surfaces couvertes passèrent de moins de 20.000 ha en 1910 à plus de 100.000

ha en 1940. Durant les années 1950, 75.000 ha supplémentaires furent plantés sous l'impulsion du gouvernement australien (De Silva 1988). La surface couverte dans les années 1970 s'élevait à 276.000 ha (De Silva 1989) et 241.000 ha dans les années 1980 (Turner 1988).

Parmi la trentaine d'espèces de termites que l'on trouve dans la région de Bogia (Pasteels & Roisin, données non publiées), douze ont réussi à s'accommoder de l'environnement particulier des cocoteraies. Elles sont inventoriées au tableau 2. Parmi celles-ci, nous concentrerons notre attention sur les espèces qui construisent leurs nids et des galeries couvertes sur les arbres. D'autres espèces construisent un nid terrestre, souvent situé au pied du cocotier et duquel émane un réseau de galeries exclusivement souterraines. Enfin, une troisième catégorie de termites cantonnent leurs colonies au bois qu'elles minent ou à des matières végétales en décomposition; par exemple une palme de cocotier tombée au sol.

Tableau 2: ensemble des espèces de termites collectées dans les cocoteraies de la côte Nord de Nouvelle-Guinée (Province de Madang).

Localisation de la société	Espèce
Nids arboricoles	*Microcerotermes biroi* (Desneux, 1905)
	Nasutitermes princeps (Desneux, 1905)
	Nasutitermes novarumhebridarum (N. & K. Holmgren, 1915)
	Nasutitermes polygynus (Roisin & Pasteels, 1985b)
	Nasutitermes sp.F.[2]
Nids terrestres	*Microcerotermes papuanus* (N. & K. Holmgren, 1915)
	Microcerotermes sp.
	Termes odontomachus (Desneux, 1905)
Matières cellulosiques en décomposition	*Glyptotermes* sp.
	Schedorhinotermes sp.
	Prorhinotermes sp.
	Coptotermes sp.

Parmi les espèces construisant des nids arboricoles, deux sont marginales en cocoteraies. *Nasutitermes polygynus* s'y observe exceptionnellement et dans ces circonstances provient généralement d'une plantation mixte cocotier-cacaoyer se trouvant à proximité (voir annexe **8**, Roisin & Pasteels 1985b). Le cacaoyer présente une morphologie beaucoup plus appropriée à la construction du nid de *N. polygynus*, qui est souvent calé entre deux ramifications, que le tronc lisse du cocotier. *Nasutitermes* sp. F, dont la biologie est encore méconnue, ne se rencontre lui aussi qu'à de très rares occasions. En définitive, parmi les termites à nids arboricoles observés dans les forêts avoisinantes, seule une, *Grallatotermes grallator*, n'a jamais été observée en plantations.

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[2] Cette espèce sera prochainement décrite sous le nom de *N. bikpelanus* (Roisin & Pasteels *sous presse*)

Espèces étudiées

Nasutitermes princeps

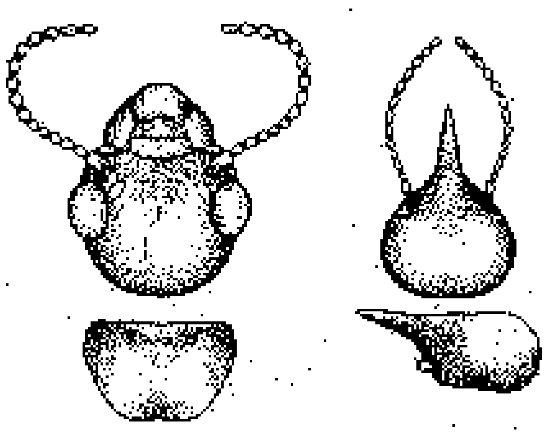

Figure 5: tête et pronotum d'un imago et tête d'un soldat de *N. princeps* (d'après Hill 1942).

Nasutitermes princeps (Desneux, 1905) se répartit sur la côte Nord de Nouvelle-Guinée de Nabire à Lae, y compris sur quelques îles proches (Manam, Karkar), ainsi que sur la côte Sud de Kaimana au Lake Murray (Roisin & Pasteels, *sous presse*; Yves Roisin, *communication personnelle*). Les ailés mesurent, ailes non comprises, de 9 à 11 mm de long; les soldats mesurent de 4.5 à 5 mm de long, dont 1.7 à 1.9 mm pour la tête; les ouvriers ont de 5.0 à 5.5 mm de long (Hill 1942). La biologie de cette espèce a été étudiée en détail par Roisin (1986). *N. princeps* construit de grands nids en carton de bois sur les troncs des arbres et une colonie est constituée d'un nid principal, contenant les sexués, et d'éventuels nids satellites, dépourvus de sexués, répartis sur des arbres avoisinants (Fig. 6). Les sexués sont localisés dans un nodule royal à cellule unique ou à cellules multiples. Près de deux tiers des colonies de *N. princeps* sont polygynes. La polygynie résulte soit du remplacement des sexués primaires soit du bourgeonnement de la colonie. Les nids les plus volumineux, qui sont aussi les plus âgés, sont toujours polygynes suggérant que le remplacement du couple fondateur de la colonie est un événement normal dans l'histoire de la colonie. Les néoténiques sont des adultoïdes, issus d'ailés présents dans les nids, ou des pseudimagos, issus de nymphes qui ont raccourci leur développement pour devenir des sexués de remplacement. *N. princeps* est remarquable par le polymorphisme de ses ailés: à côté d'ailés normaux se rencontrent des ailés à ailes courtes appelés microimagos (Roisin & Pasteels 1985a) (Fig. 7), incapables de voler mais prêts à se développer en sexués fonctionnels dans le nid principal ou dans un nid satellite. Le mode de reproduction par bourgeonnement, suggéré par le fort taux de polygynie, est corroboré par la présence en nature de nids voisins polygynes, mutuellement non-agressifs et présentant de grandes similarités dans la composition de la sécrétion défensive de leurs soldats, suggérant une similarité génétique et une origine commune (Roisin *et al.* 1987). *N. princeps* a été décrit attaquant des cacaoyers (*Theobroma cacao*) (Szent-Ivany 1963).

Figure 6: Colonie polydome de *N. princeps* avec le nid principal (A) et sa calie (B).

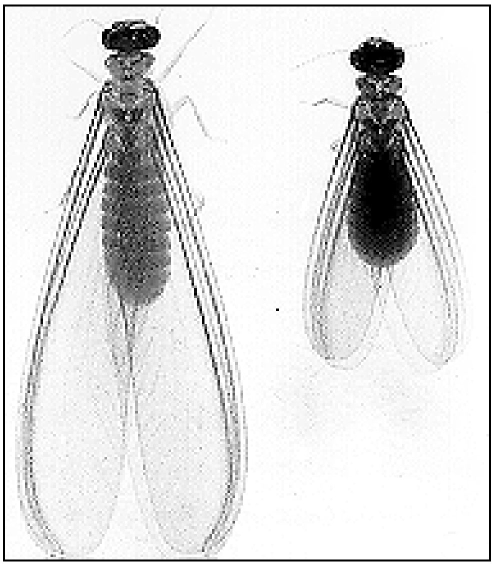

Figure 7: Ailé normal et microimago de *N. princeps* (d'après Roisin & Pasteels 1985a).

Nasutitermes novarumhebridarum

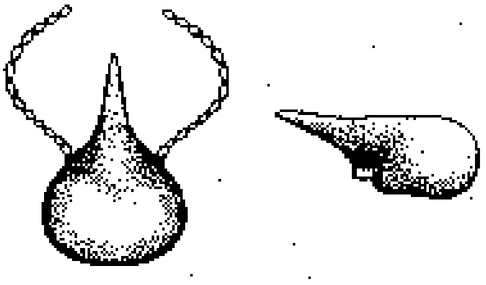

Figure 8: tête d'un soldat de *N. novarumhebridarum* (d'après Hill 1942).

Les *Nasutitermes novarumhebridarum* (N. & K. Holmgren, 1915) sont très répandus géographiquement: Nouvelle-Guinée, Irian Jaya, Schouten Islands, archipel de Bismarck, Nouvelle Calédonie Roisin & Pasteels, *sous presse*; Yves Roisin, *communication personnelle*). Les ailés mesurent, ailes non comprises, de 7.0 à 8.5 mm de long (14.0 à 16.5 mm avec les ailes); les soldats mesurent de 4.0 à 4.5 mm de long, dont 1.7 à 1.9 mm pour la tête; les ouvriers ont de 5.0 à 5.5 mm de long (Hill 1942). Les nids en carton de bois sont arboricoles en Nouvelle-Guinée mais parfois construits au sol aux îles Salomon (Harris & Brown 1958). *N. novarumhebridarum* s'observe souvent sur des arbres frappés par la foudre ou endommagés durant la guerre (Szent-Ivany 1956). Les colonies contiennent toujours un couple de sexués imaginaux et se propagent apparemment exclusivement par essaimages (Roisin & Pasteels 1987a). Les sexués de remplacement sont des ergatoïdes issus d'ouvriers.

Microcerotermes biroi

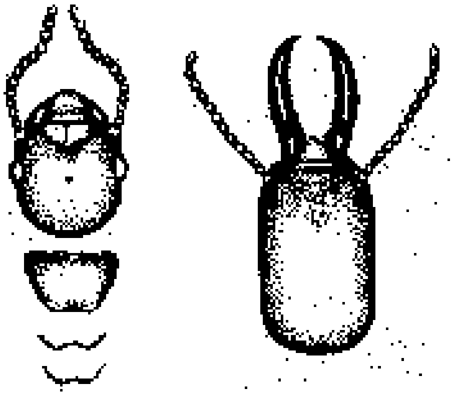

Figure 9: tête et pronotum d'un imago et tête d'un soldat de *M. biroi* (d'après Hill 1942).

Microcerotermes biroi (Desneux, 1905) a une large distribution couvrant l'ensemble de la Nouvelle-Guinée, la Nouvelle-Bretagne, les îles Salomon, les îles Samoa et s'étendant peut-être jusqu'en Nouvelle-Zélande (Hill 1942, Roisin & Pasteels *données non publiées*). *M. biroi* construit un nid en carton de bois sur les troncs d'arbres. Les soldats possèdent de longues mandibules (figure 9). Les ailés mesurent, ailes non comprises, de 5.2 à 6.5 mm de long (9.0 à 10.6 mm avec les ailes); les soldats mesurent de 5.2 à 6.5 mm de long, dont 2.9 à 3.1 mm pour la tête, mandibules comprises (Hill 1942, Héraoui 1987). Cette espèce s'attaque aux constructions en bois (*obs. pers.*). La biologie de cette espèce, en particulier son mode de reproduction a été étudiée à l'occasion du présent travail (chapitre **4**).

Organisation de la thèse

Les résultats acquis lors du présent travail sont présentés sous la forme de 5 articles rédigés en anglais et constituant autant de chapitres. Les textes originaux de ces articles sont proposés dans leur intégralité. La présentation des textes a cependant été uniformisée et les références bibliographiques ont été regroupées en une liste commune.

La compréhension de la structure et de la dynamique de la communauté de termites à nids arboricoles requiert une bonne connaissance de la biologie des espèces, des interactions entre colonies, de l'importance de la prédation et des réponses de chacune des espèces aux variations de l'environnement physique.

La biologie des espèces, la structure de la communauté et la dynamique des interactions interspécifiques sont présentées au chapitre 2 —intitulé "*Structure and dynamics of the arboreal nesting termite community*"— complété par des informations non publiées portées en annexes **1** à **9**. Le mode de reproduction et la dynamique de colonisation de *M. biroi* sont examinés au chapitre 3 — intitulé "*Reproductive mechanisms and dynamics of habitat colonization in Microcerotermes biroi*"— et confrontés à ceux des deux *Nasutitermes* dans le but d'évaluer le rôle des stratégies de reproduction dans l'organisation de la communauté.

Les divers arrangements spatiaux des arbres rencontrés en cocoteraies entraînent des fluctuations du microclimat ainsi que des variations dans la quantité de nourriture et de sites de nidification disponibles. La réponse des espèces aux variations de l'habitat est abordée au chapitre 4, "*Environmental influences on the arboreal nesting termite community in New Guinean coconut plantations*".

Les conséquences des interactions entre colonies homospécifiques et des interférences causées par les principaux prédateurs —à savoir les fourmis—, sont considérées respectivement aux chapitres 5 ("*Intraspecific interactions in a community of arboreal nesting termites*") et 6 ("*Interference of ants with arboreal-nesting termites in New Guinean coconut plantations*").

L'ensemble des résultats est finalement intégré dans une discussion générale sur l'organisation de la communauté de termites arboricoles en cocoteraie (chapitre 7).

2. Structure and dynamics of the arboreal nesting termite community

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Maurice Leponce, Yves Roisin and Jacques M. Pasteels

King Léopold III Biological Station, Laing Island, Papua New Guinea, contribution n°286

Abstract.

Whereas ant mosaics have been widely recognized and described in tropical ecosystems, data on space partitioning among arboreal termite colonies are rudimentary. During a long term field study in New Guinea, the distribution of arboreal termite species in coconut plantations as well as the extent and dynamics of competition between them were investigated. The three dominant species, *Microcerotermes biroi*, *Nasutitermes princeps* and *N. novarumhebridarum*, feed on the same items but never exploit the same tree. The resulting distribution pattern is a mosaic with two peculiarities. First, some extended areas around *N. princeps* colonies appear unexploited, as this species practices interference competition on a wide scale, defending large territories inter- and intraspecifically. Second, interspecific relations are asymmetrical. In some plantations, large colonies of *N. princeps* expand their territory by destroying colonies of *M. biroi*, but when the pressure of *N. princeps* is relaxed, dense populations of colonies of *M. biroi* can recolonize the trees in a few years' time. Territorial boundaries may thus change relatively fast. *N. novarumhebridarum* often colonizes dead trees and interferes less with the other species. These facts are consistent with each species' reproductive investment strategy. Hypotheses are proposed to explain how the dominant species can coexist, even in long established plantations.

Key words: Isoptera; *Nasutitermes*; *Microcerotermes*; interspecific competition ; mosaic distribution; coconut plantations.

Introduction

Ants and termites are major constituents of terrestrial ecosystems. In many ant communities, interference competition is widespread inter- or intraspecifically (reviewed in Hölldobler &

Wilson 1990). In some species, each colony defends an absolute territory against all intruders, as *Oecophylla* weaver ants do (Hölldobler 1979). This is generally considered to represent true territoriality (Levings & Traniello 1981). Some species which exploit persistent resources, such as seed patches, by means of long-lasting trunk trails, defend only the vicinity of their nest, trails and food sources (Hölldobler 1976, Levings & Traniello 1981). Among the ants that do not defend an absolute territory, many species defend at least their food sources (Adams & Traniello 1981). Other species interfere with competitors by preventing them from leaving their nest to forage (Möglich & Alpert 1979, Hölldobler 1982).

In many native and agricultural ecosystems of subtropical and tropical regions, canopies are dominated by a few ant species which exclude each other from their absolute, three-dimensional territories. The resulting patchy distribution has been termed "ant mosaic" (Leston 1973, 1978; Majer 1976a, b; Jackson 1984; review in Majer 1993). With each dominant species is associated a distinct assemblage of subordinate ones. Within a few years' time, the distribution of dominant species may show fluctuations of importance for the whole community (Brown 1959b, Greenslade 1971).

Ecologically, termites differ from ants in several ways. The basic diet of most termites is dead wood, whereas ants may exploit a large variety of food sources, especially insect prey. Consequently, foraging strategies are not as diverse in termites as in ants. Whereas the most primitively organized termite colonies remain small and live within a piece of wood that provides both shelter and food, the large colonies of the Termitidae usually build a definite nest from which foragers exploit food sources through a network of long-lasting trails. The persistence of such trails suggests that Termitidae colonies may competitively interfere with strangers along these trails and around discovered resources to secure their exclusive exploitation. However, interference competition could go some steps further: a colony could keep other colonies out of its whole territory, even though some areas are not being exploited.

On the contrary, if interference competition were milder, one could observe peaceful coexploitation of food sources.

Field studies of competition between termite colonies are scarce. Nest overdispersion, providing indirect evidence for both intra- and interspecific competition, has been found in several mound building termite communities of Australia (Wood & Lee 1971, Spain *et al.* 1986). Interference competition is suggested by interspecific aggressivity, which seems to be very common (Thorne 1982a review in Thorne & Haverty 1991) although avoidance (Nel 1968) or even obligatory inquilinism (Emerson 1938) are sometimes observed. Jones & Trosset (1991), using toilet paper rolls as baits, observed an aggressive displacement of *Gnathamitermes perplexus* from bait sites by *Heterotermes perplexus*. LaFage (*in* Su & Scheffrahn 1988), reported that in some areas of New Orleans, *Coptotermes formosanus* is displacing completely the native *Reticulitermes* species. In a Panamanian mangrove, Levings & Adams (1984, Adams & Levings 1987) mapped the obligatory above-ground foraging trail system of colonies of two arboreal nesting *Nasutitermes* species. Mutually aggressive colonies filled nearly all the available space in a mosaic pattern. Gaps in termite distribution were mostly found where neighboring trees lacked aerial connections. Fights were sometimes observed near territorial boundaries and most often resulted in trail divergence, although in one case they led to the elimination of a small *N. nigriceps* colony by a neighboring *N. corniger* colony. This study thus provided good evidence for the presence of territoriality and interference competition in *Nasutitermes*, but left several questions unsolved. Can the mosaic pattern be generalized to other tropical ecosystems, and involve other termite genera ? What is the extent of interference competition, and do all dominant species behave similarly ? Do termite mosaics change with time as ants mosaics do ?

Three arboreal nesting termites live in New Guinea coconut plantations: *Microcerotermes biroi* (Desneux, 1905) and *Nasutitermes novarumhebridarum* (N. and K. Holmgren, 1915) whose colonies are small and reproduce by nuptial flights (Roisin and Pasteels 1987a, Chapter **4**) and *Nasutitermes princeps* (Desneux, 1905) whose colonies are large and reproduce frequently by budding (Roisin and Pasteels 1986a, Roisin 1987). A previous study (Roisin *et al.* 1987) indicated that the two most abundant species, *N. princeps* and *M. biroi*, never occur on the same tree, suggesting a competitive exclusion. In order to study each species' territoriality and the role of interspecific interactions in shaping the community structure, we undertook a long-term field study. First, we studied the community structure and the colony organization of each species in 10 randomly selected plots. Second, we followed during 3-10 years the dynamics of territorial interactions in two sites: one in which *N. princeps* colonies were in natural expansion and another in which *N. princeps* colonies were artificially weakened.

Materials and methods

The study sites were located in Bogia district, Madang Province, Papua New Guinea, along the coastline of Hansa Bay (approximately 4°10'S, 144°50'E).

Community composition and structure.

The abundance and distribution of arboreal-nesting termites were studied by a single sampling in 10 quadrats of approximately one hectare (100m x 100m) randomly selected in coconut monocultures (plantation pattern in 9m x 9m squares or denser). The coconut trees within the plots were marked with paint according to a row/column coordinate system. Every coconut tree within the quadrat was checked for current or past presence of carton-covered galleries and nests of arboreal termites. The identity of the nest or gallery original builder was determined according to the structure of the nest or gallery (markedly different between *Microcerotermes* and *Nasutitermes*). Current occupiers were identified by opening the construction. *Nasutitermes* nest volumes were estimated considering the nest equivalent to an ellipsoid of revolution centered on the tree trunk. The three axes of the ellipsoid were measured; the intersection between the ellipsoid and the cylindrical trunk of the coconut tree was subtracted from the ellipsoid volume. *M. biroi* nest volumes were estimated considering the nest equivalent to a sector of a hollow cylinder([3]). Colonies were delineated by several complementary methods: aggressiveness tests between individuals found on neighbor trees, mapping of colonies and, in the case of *Nasutitermes*, analysis of soldier defensive secretion (for details see Roisin *et al.* 1987). Every termite nest was measured with a tape measure.

Dynamics of territorial interactions between *N. princeps* and *M. biroi*.

The dynamics of competitive interactions between *M. biroi* and *N. princeps* was studied in four additonal plots mapped at intervals of 6 to 12 months: plot Potsdam #1a (1.1 ha), followed for 10 years, where *N. princeps* nests were suppressed or weakened by orphaning (queen removal); neighbor plot Potsdam #1b (0.44 ha), followed for 3 years, which remained unmanipulated; plot Awar #2a (3.1 ha), followed for 4 years, where *N. princeps* nests were exceptionally abundant and in expansion; neighbor plot Awar #2b (0.63 ha) where *M. biroi* was the most abundant species, unaffected by the progression of *N. princeps* when mapping was undertaken, and followed for 4 years.

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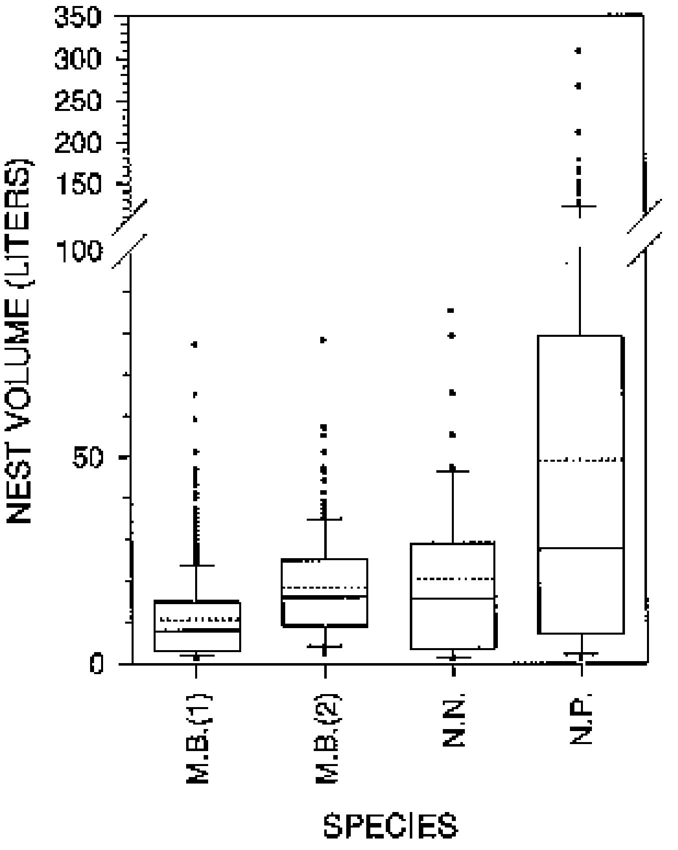
[3] For more details see appendix **1**.

Results

Community composition and structure.

The analysis of our data from the 10 randomly selected sites reveals that 56 ± 11 % (average ± standard deviation) of the coconut trees are occupied by arboreal termite galleries and nests. The relative abundance of the different species are the following: *M. biroi*: 87 ± 10 % (nests: 54 ± 16 %; galleries only: 33 ± 9 %); *N. princeps*: 10 ± 8 % (nests: 2 ± 1 %; galleries only: 8 ± 7 %); *N. novarumhebridarum*: 3 ± 3 % (nests: 2 ± 2%; galleries only: 1 ± 1 %).

Nests of *M. biroi* were generally smaller than those of *N. princeps* and *N. novarumhebridarum* (Fig. 10). The volume of *M. biroi* individual nests is on average 11 liters (maximum observed: 77 liters, median= 8 liters, n=871). When several nests of *M. biroi* were present on the same tree, their volumes add up on average to 18 liters (maximum: 78 liters, median= 16 liters, n=187). A *M. biroi* colony occupies on average three trees; one supporting the nest containing the reproductives, another supporting one or several nest(s) without reproductives and a third with covered galleries only (Fig. 11). *N. novarumhebridarum* average nest volume is 20 l. (maximum: 85 liters, median= 15 l., n=48) (Fig.



▲**Fig. 10.** Box plots of arboreal nest volumes. M.B., *M. biroi*, total nest volume per tree when a single nest (1) or up to three nests (2) was/were present; N.N.: *N. novarumhebridarum*; N.P.: *N. princeps*; individual nest volume. The horizontal lines inside the box represent the median (solid line) and the average (dotted line). The horizontal ends of the box represent the quartiles. The fences are defined as 10% and 90% percentiles. Extreme values, data values outside the fences, are represented by dots.

10). *N. novarumhebridarum* colonies were generally monodomous (i.e., they build a single nest) and occupy on average three trees with covered galleries. However, in about 15% of the cases two nests were found, always on a single tree. *N. princeps* colonies build large nests of up to 300 liters (average volume: 49 liters, median= 28 liters, n=134) (Fig. 10). They were polydomous (i.e., composed of multiple nests) in about 30% of the cases and in that instance nests were always on separate trees. Their foraging gallery network spreads on large areas. Abandoned galleries were often present on trees at the edge of the area exploited by a colony. For instance, on Fig. 11, a *N. princeps* nest (P) of 107 liters was surrounded by a network of occupied galleries reaching 11 trees whereas 8 trees bore abandoned galleries.

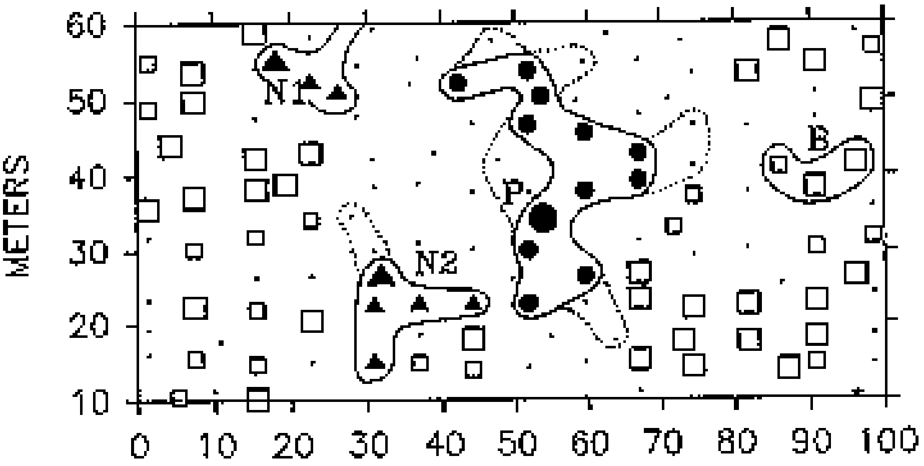


Fig. 11: Detail of a representative quadrat (Potsdam #4) showing the horizontal distribution of nests and galleries of the three arboreal-nesting species. Squares: *M. biroi*. Circles: *N. princeps*. Triangles: *N. novarumhebridarum*. Large symbols: nests and covered galleries; small symbols: galleries only. Solid lines: presumed territory areas at the time of mapping. Dotted lines delineate trees with marks of previous occupation.

N. princeps, *N. novarumhebridarum* and *M. biroi* fed on the same plant material, such as dead palm leaves that were still attached to the trees or on the ground, coconut husks, or dead inflorescences([4]). Food sources exploited by *N. princeps* were interconnected by epigeal galleries. Hypogeal galleries could be found when dead vegetable matter was in direct contact with humus. These hypogeal galleries were found in the top 5 centimeters of soil. *N. novarumhebridarum* and *M. biroi* shared similar habits, although the galleries of *M. biroi* were narrower than those of the *Nasutitermes* species. The development of the gallery

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[4] for more details see appendix **2**

network increased with the volume of the nest([5]). None of the species attacked healthy coconut trees.

Table 3 shows a very highly significant mutual exclusion of the three species from any single coconut tree. The four observed cases of joint presence of *M. biroi* and *N. princeps* on a tree corresponded to a nest of *M. biroi* nest with carton covered galleries of *N. princeps* running along its side. We will describe the interactions between these two species below.

Table 3. Observed occurrence of the three arboreal termite species on coconut trees. The expected occurrence in case of mutual independence among all variables is under parentheses.

	without *N. princeps*		with *N. princeps*		Total
	without *N.novarum-hebridarum*	with *N.novarum-hebridarum*	without *N.novarum-hebridarum*	with *N.novarum-hebridarum*	
without *M. biroi*	767 (832.77)	33 (16.34)	109 (58.74)	0 (1.15)	909
with *M. biroi*	802 (738.41)	0 (14.49)	4 (52.08)	0 (1.02)	806
Total	1569	33	113	0	1715

three-dimensional $\chi^2 = 131.72$, d.f.= 4, P<.001

Dynamics of territorial interactions between *N. princeps* and *M.biroi*.

The dynamics of the territorial interactions between *N. princeps* and *M. biroi* was documented in two sites evolving in opposite directions: in one case (Potsdam #1a), experimental weakening of *N. princeps* colonies allowed a progression of *M. biroi*; in the other (Awar #2a), a very dense population of *N. princeps* expanded its territory at the expense of *M. biroi*. In both cases, comparative data were collected from neighboring areas, respectively Potsdam #1b, in which *N. princeps* nests were left undisturbed, and Awar #2b, which was out of reach for *N. princeps* invaders when the study of the Awar plots was undertaken.

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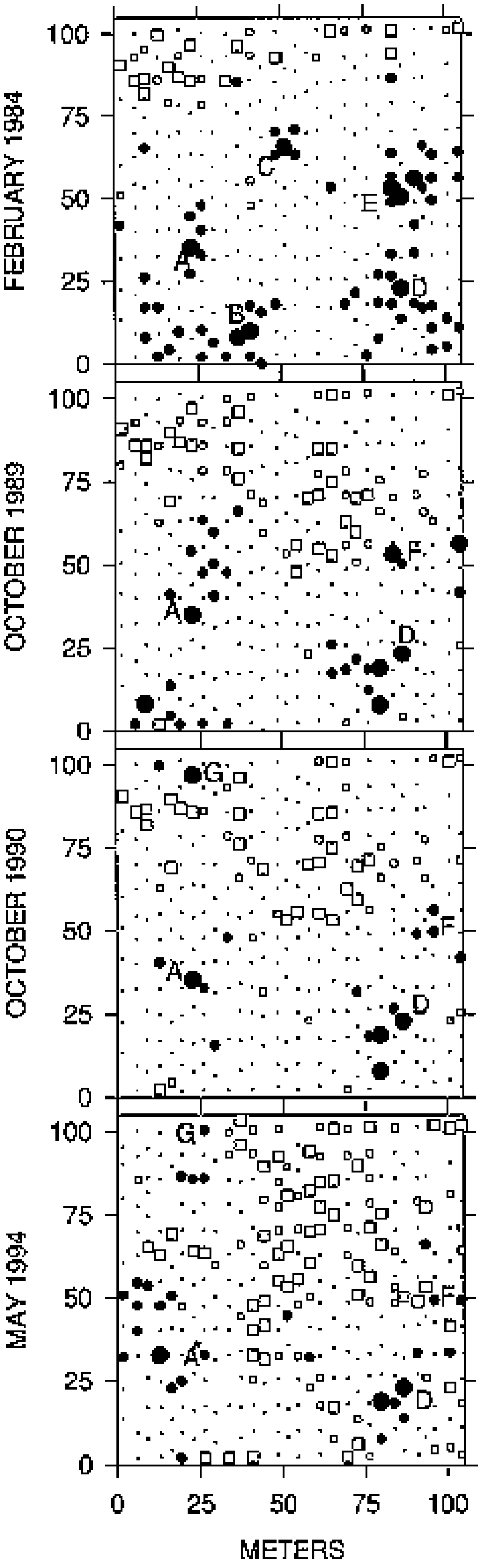
[5] for more details see appendix **3**



< **Fig. 12.** Dynamics of colonization by *M. biroi* and *N. princeps* in Potsdam #1a between February 1984 and May 1994. Symbols for species: Squares: *M. biroi*, Circles: *N. princeps*. Dots: coconut trees. Large symbols: arboreal nests. Small symbols: arboreal galleries. Manipulations to *N. princeps* colonies E, C, B caused their disappearance (for more details, see Fig. 13), colonies F and G extend outside of the plot.

In Potsdam #1a, maps of the colonization of the plantation were made for 10 years (Fig. 12). In 1983, eight nests of *N. princeps*, belonging to five different colonies (A-E), occupied 21% of the trees present; *M. biroi* occupied only 10% of the trees. Large areas situated around the *N. princeps* colonies were almost unexploited. The *N. princeps* population was then experimentally weakened through nest orphaning or removal (see Fig. 13). Between February 1984 and October 1989, *N. princeps* nests E (orphaned in May 1983) and C (orphaned in June 1986) died and nest B was removed (in April 1989). Meanwhile, *N. princeps* colony A declined, probably because the coconut tree supporting the nest died. When the tree fell down in April 1992, the nest was abandoned and replacement reproductives appeared in a nest built on a tree 10 m away. As shown quantitatively on Fig. 13, the removal of *N. princeps* colonies was followed by a re-establishment of *M. biroi*. Many trees surrounding the *N. princeps* colonies were still unoccupied, but the total proportion of unoccupied trees dropped from 68% in 1984 to 52% in 1994, due to the establishment of a dense population of *M. biroi* nests, especially in the central area of the plot (Fig. 12). In the neighboring plot Potsdam #1b, of 0.44 ha, which was left undisturbed, *M. biroi* and

N. princeps occupied in April 1991 respectively 45% and 19% of the trees present (against, respectively, 24% and 5% in Potsdam #1a at the same time). A large, old, *N. princeps* nest (172 liters), largely invaded by ants, was abandoned between April 1991 and May 1992 and replacement reproductives appeared in the satellite nest of the colony (72 liters in 1992) which increased in size afterwards (96 liters in 1994). Another *N. princeps* nest did not change much in size throughout the period (1991: 37 liters, 1992 and 1994: 48 liters) and satellite nests appeared here and there but never lasted. A single nest of *M. biroi* was invaded by *N. princeps*. Globally, the proportions of trees occupied by *M. biroi* and *N. princeps* remained fairly constant between 1991 and 1994 in Potsdam #1b.

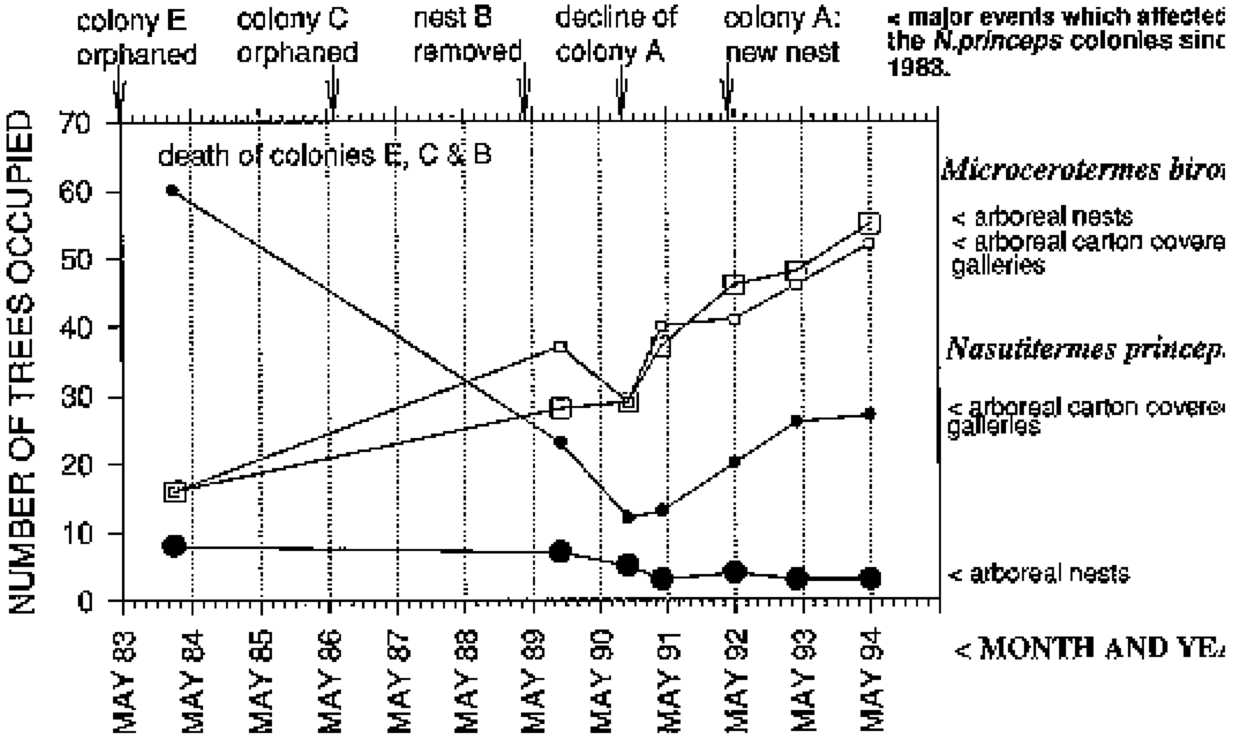


Fig. 13. Effect of the relaxation of *N. princeps* pressure on *M. biroi* in Potsdam #1a: number of trees occupied by either species between February 1984 and May 1994.

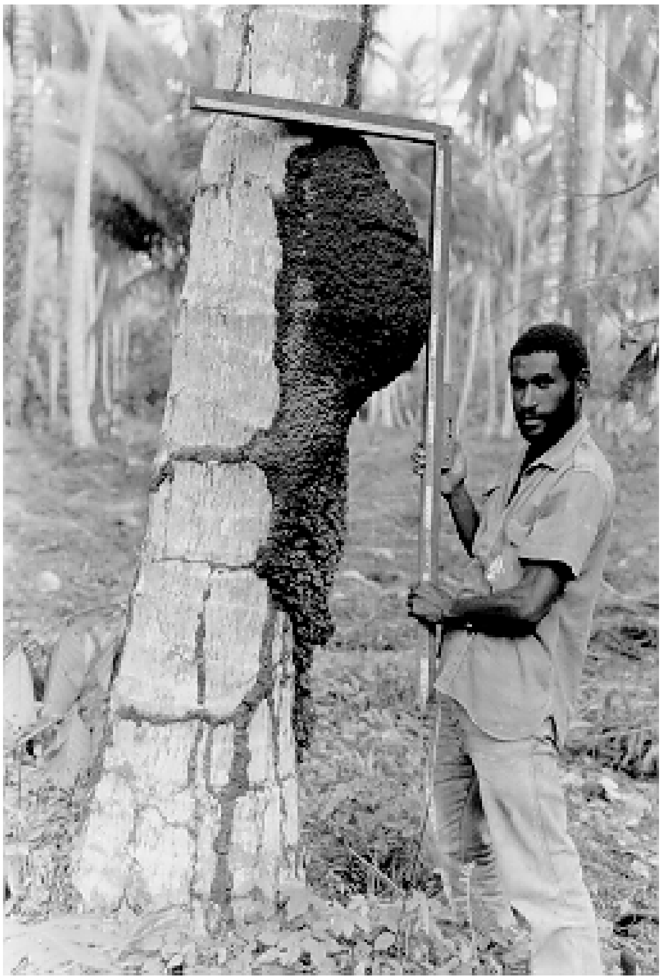


Fig. 14. Nest of *M. biroi* invaded by *N. princeps*. The ellipsoidal *N. princeps* nest can easily be distinguished over the top of the flat *M. biroi* nest.

Awar #2a is an area of 3.1 ha which is remarkable for its exceptionally large population of *N. princeps* nests. All those nests were mutually non aggressive, and very few trees were left unoccupied. The surroundings of Awar #2a were largely dominated by *M. biroi* (cf. Awar #2b, see below) as well as originally Awar #2a itself. Indeed, 60% of the trees occupied in May 1990 by *N. princeps* also supported remnants of nests or carton-covered galleries built by *M. biroi* (Fig. 14). In Awar #2a, *N. princeps* clearly progressed at the expense of *M. biroi* between May 1990 and May 1992 (Fig. 15). Fig. 16 shows quantitatively the increase in the number of trees colonized by *N. princeps* (from 95 to 134 nests) and the correlated decrease of *M. biroi* (from 46 to 12 nests) during that period. After the peak of nest density in 1992, a severe decrease was observed after two unusually dry seasons([6]) during which food on the ground was desiccated and accidentally burned by fires. In July 1993, 42 of the 134 *N. princeps* nests present in May 1992 had fallen down to the ground; among them 83% (35/42) had a volume under average and were probably satellite nests. In May 1994, 58 other nests, of which 45 (78%) had a volume under average, were missing. Five of them had been destroyed by a fire.

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[6] for more details about the climate see appendix **4**

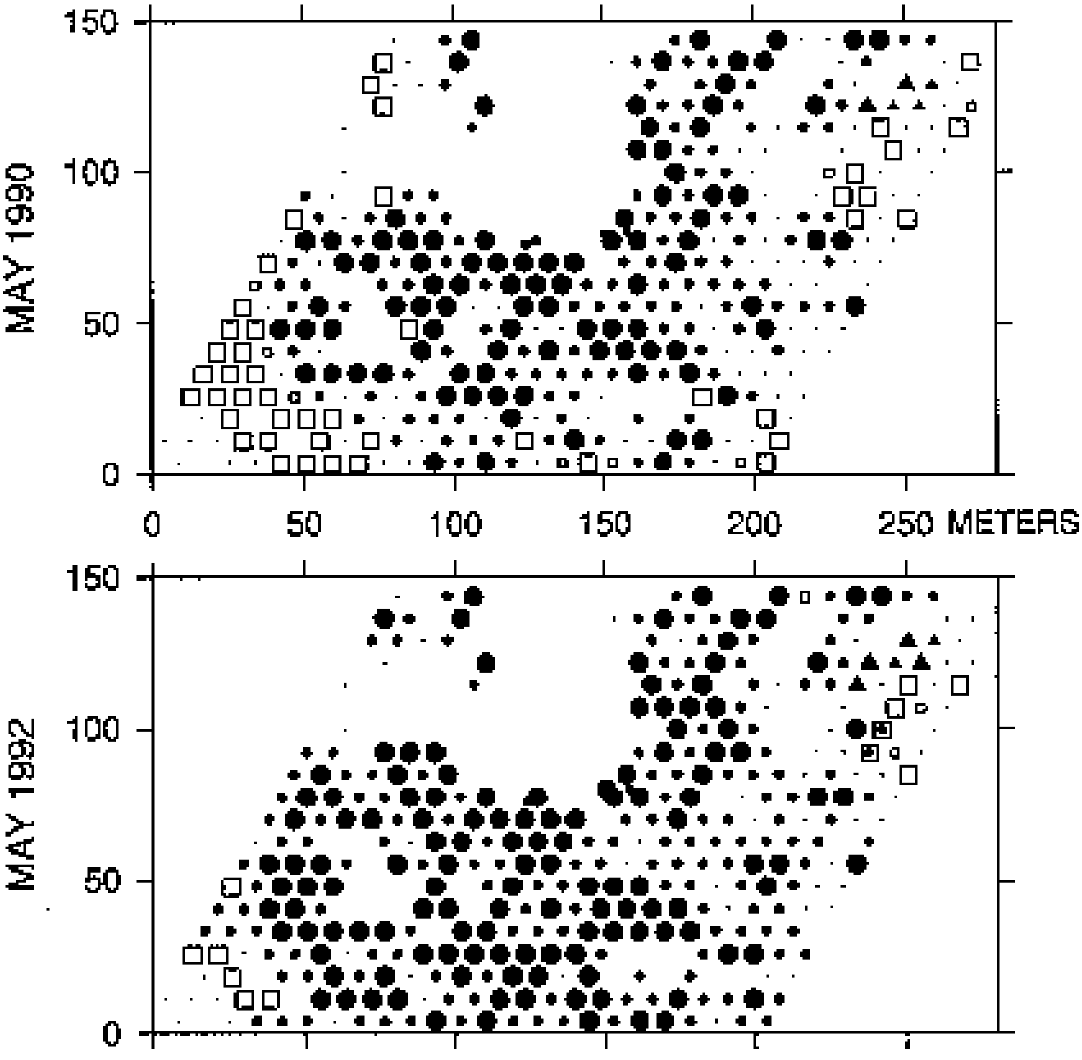

Fig. 15. Dynamics of colonization by *M. biroi*, *N. princeps* and *N. novarumhebridarum* in Awar #2a between May 1990 and May 1992. Symbols for species: Squares: *M. biroi*, Circles: *N. princeps*, Triangles: *N. novarumhebridarum*. Dots: coconut trees. Large symbols: arboreal nests. Small symbols: arboreal galleries.

The neighboring plot Awar #2b was not reached by the progression of *N. princeps* until May 1991. In this plot, *M. biroi* was the most abundant species in October 1990, occupying 56% of the trees. In the absence of competition with *N. princeps*, the number of trees occupied by *M. biroi* increased by 5% between October 1990 and May 1991, while the overall volume of *M. biroi* nests increased by 8%. As the invasion of *N. princeps* coming from nearby plot Awar #2a reached Awar #2b, 9 nests of *M. biroi* out of 40 died and were replaced by *N. princeps* between 1991 and 1992, as well as 8 nests out of 34 between 1992 and 1993. Between 1993 and 1994, a slight recovery of *M. biroi* followed the breakdown of the *N. princeps* population.

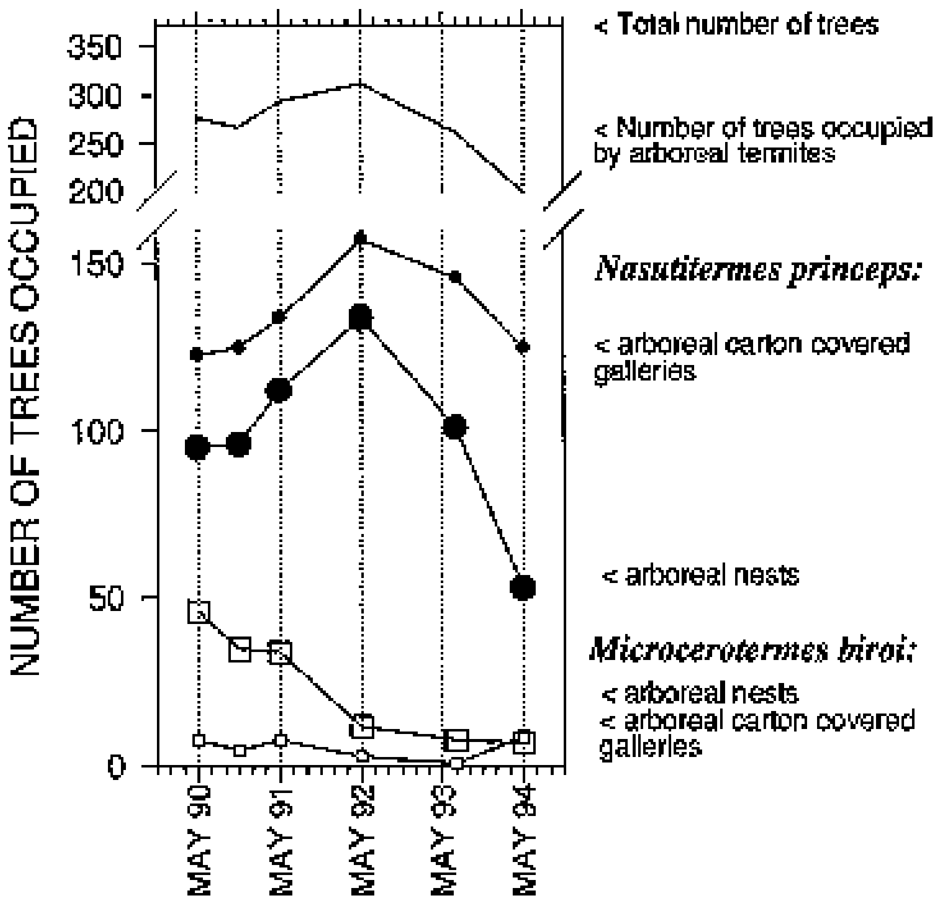

Fig. 16. Effect of the expansion of *N. princeps* on *M. biroi* in Awar #2a: number of trees occupied by either species in May 1990 and May 1992.

Occurrence of direct interspecific contests.

Repeated watching of boundaries between areas occupied by *M. biroi* and *N. princeps* allowed us to observe twice the invasion of a *M. biroi* nest by *N. princeps*. On June 1st, 1991, a coconut tree was found supporting both a nest of *M. biroi* (estimated volume: 26 liters) and a covered gallery of *N. princeps* which probably issued from a nest (estimated volume: 85 liters) situated 20 m away. The *N. princeps* covered gallery ran along one side of the *M. biroi* nest and reached the crown of the tree. One week later, the gallery was found empty and damaged by rain. On June 17, the gallery was still damaged but contained *N. princeps* near ground level. Dead bodies of both species lay on the trunk and were carried away by *Oecophylla* ants. A clicking sound, produced by *M. biroi* soldiers banging their head against the substrate(7), could be heard 2 m away. The odor of the defensive secretion of *N. princeps* soldiers could be smelt near the nest surface. Live *N. princeps* were seen in some parts of the nest. During the following days, the old *N. princeps* galleries were repaired and new ones

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[7] cf. annexe **5** Fig. **41**

built all around the *M. biroi* nest and on its surface. No more corpses could be observed outside the nest or covered galleries. The head banging of *M. biroi* could be heard continuously but became fainter and fainter until June 23, then it stopped. On June 26, the galleries were occupied by *N. princeps* and no *M. biroi* was seen any more.

Another invasion of a nest of *M. biroi* by *N. princeps* was discovered on 31 March 1993. Numerous dead bodies of both species were found on the tree trunk, giving additional evidence for the occurrence of battles outside the nest ([8]). *N. princeps* soldiers were found on patrol on the lower part of the tree trunk and on the nest. Some penetrated into the nest by small openings in the outer wall ([9]). The next day, *N. princeps* started building covered galleries around the nest ([10]). After one week, the head banging of *M. biroi* stopped. A dissection of the nest at that time showed that the chamber walls were perforated, allowing the *N. princeps* to penetrate deep into the structure ([11]). Dust from the perforated nest walls covered the floor of the chambers. Small groups of live *M. biroi* were found around the royal cell which still contained eggs but no reproductives ([12]). The rest of the nest contained numerous dead bodies.

When workers and soldiers of *N. princeps* invaded a nest of *M. biroi*, they remodel it according to their own needs. Nests of *M. biroi* are made of small chambers communicating by elliptical orifices whose size corresponds exactly to the soldier head capsule thickness and is too small to allow the passage of *N. princeps* soldiers and large workers. By contrast, this latter species builds widely open chambers allowing several termites to pass at a time from one chamber to another (Deligne & Pasteels 1982).

Although we never had the opportunity to observe the progress of the invasion of *M. biroi* nests by *N. novarumhebridarum*, we gathered evidence that this species also interacts aggressively with *M. biroi*. A few recently invaded *M. biroi* nests were found with dead bodies of both *M. biroi* and *N. novarumhebridarum* inside and outside them. Galleries of *N. novarumhebridarum* were found surrounding *M. biroi* nests as observed with *N. princeps*. Furthermore, some *N. novarumhebridarum* nests were found built over old *M. biroi* nests.

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[8] cf. appendix **5** , Fig. **42**

[9] cf. appendix **5** , Fig. **43**

[10] cf. appendix **5** , Fig. **44**

[11] cf. appendix **5** , Fig. **45**

[12] cf. appendix **5** , Fig. **46**

Discussion

The distribution of arboreal nesting termites in New Guinean coconut plantation is reminiscent of the mosaic pattern shown by ants in many tropical ecosystems (Leston 1973, 1978, Room 1975 Majer 1976a, b; Jackson 1984; review in Majer 1993) and by arboreal *Nasutitermes* in Panamanian mangroves (Levings & Adams 1984; Adams & Levings 1987). Dominant species occupy territories which do not overlap. However, a peculiarity of the termite mosaic described here is the presence of large unoccupied areas surrounding *N. princeps* colonies. That such areas were not occupied because they were unsuitable for termite colonization is unlikely: in experimental plot Potsdam #1a, unexploited areas were quickly colonized by dense populations of colonies of *M. biroi* once neighboring *N. princeps* nests were removed (Fig. 12). Aggressive interactions between members of antagonistic colonies may account for the presence of a "no- termites' land" between territorial boundaries. This phenomenon is well-known in ants, although unoccupied areas between ant territories are usually narrow corridors (Leston 1973; Hölldobler 1979; Hölldobler & Lumsden 1980). In the Panamanian mangroves studied by Levings & Adams (1984; Adams & Levings 1987), almost all trees were part of the territory of an arboreal *Nasutitermes* colony unless they lacked aerial connections with other trees and were thus isolated at high tides; narrow gaps were generally present between territorial boundaries of different colonies. Jones (1993) observed repeated battles between subterranean colonies of *Heterotermes aureus* similarly followed by the establishment of an unexploited gap 2-3 meters wide between their foraging areas. In New Guinean coconut plantations, there are no physical barriers to prevent termite foragers from walking from one tree to the next. The fact that large areas appear unoccupied by arboreal termites around colonies of *N. princeps* suggests that other homo- or heterospecific colonies were nevertheless excluded from them, even though they may be left unexploited for some time. This hypothesis is supported by the common finding of recently abandoned galleries of *N. princeps* in the no termites' land, which suggests that the areas actually exploited by a colony of *N. princeps* may fluctuate quickly ([13]). This strategy could ensure priority access to new food sources (e.g., dead palm leaves) as they become available within the territory. Perhaps more importantly, a large defended territory may be necessary to ensure colony survival if the density of suitable food items fluctuates in time or space. Interestingly, the large population of mutually non aggressive *N. princeps* nests found in Awar #2a (Fig. 15), which probably constituted an unicolonial system, was very dense and left almost no unexploited tree within its range. This suggests that the carrying capacity of the habitat may be substantially higher than the density observed when colonies are surrounded by competitors.

Both *N. princeps* and *M. biroi* are territorial in the sense that they exclude other colonies from an area which exceeds the immediate vicinity of their nest and food sources. Territories of *M. biroi* may not extend much further than the trees supporting the nest and the foraging galleries, reminiscent of harvester ants' trunk trail territories (Hölldobler 1976), but *N. princeps* colonies seem to defend their potential foraging grounds well beyond their food sources. This strategy requires sophisticated mechanisms of communication of alarm and short- and long-range recruitment, which some arboreal *Nasutitermes* species, including *N. princeps*, possess([14]) (Traniello 1981, 1982; Roisin *et al.* 1990), precisely like *Oecophylla* ants (Hölldobler & Wilson 1977, Hölldobler 1979). That interference competition is widely used by *N. princeps* was further demonstrated by direct observations of interspecific battles, in which nests of *M. biroi* were invaded by *N. princeps*. Similar events probably also occur, though less frequently, between *M. biroi* and *N. novarumhebridarum* ([15]). By contrast, no evidence was ever found of *M. biroi* expelling either *Nasutitermes*, although *M. biroi* is able

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[13] cf. appendix **6** Fig. **47**

[14] The defensive secretion of *N. princeps* soldiers has a pheromonal role. By contrast, such pheromonal effect has not been observed in *N. novarumhebridarum* (for more details see appendix **7**).

[15] and also between *M. biroi* and *N. polygynus* (see appendix **8**).

to recolonize areas on which *Nasutitermes* has lost control. The relationship between *M. biroi* and *Nasutitermes* species (especially *N. princeps*) thus appears to be asymmetrical. Our results suggest that *M. biroi* is a pioneer species, which is able to invade a habitat with a dense population of new, small colonies, whereas *N. princeps* forms large colonies that increase in size and extend their territory progressively by budding. This assumption is consistent with our knowledge of each species' reproductive strategy. During the wet season, we commonly observed *M. biroi* alates engaged in massive nuptial flights, and incipient colonies were very common in dead wood. In coconut plantations, most *M. biroi* colonies were monogynous and headed by the primary reproductives (Chapter **4**). By contrast, only one nuptial flight of *N. princeps* was observed in years of field work, and neither signs of recent flights (e.g. alates drowned in water ponds or caught in spider webs) nor incipient colonies of *N. princeps* were ever found. *N. princeps* therefore appears to be a less efficient long distance colonizer than *M. biroi*. Nests of *N. princeps* are often polydomous (Roisin *et al.* 1987), and multiple replacement reproductives readily develop in orphan nests (Roisin & Pasteels 1986a). The fact that more than 60% of the *N. princeps* colonies are polygynous in coconut plantations suggests that colony reproduction by budding is frequent in this species (Roisin & Pasteels 1986a; Roisin 1987). Furthermore, many colonies produce, instead of fully developed alates, microimagos (Roisin & Pasteels 1985a), unable to fly, but ready to become secondary reproductives in satellite nests. *N. novarumhebridarum* was less abundant and often occupied dead or dying trees; its mature colonies seem to invest preferentially in the production of alates, which can colonize new sites at a distance, rather than in colony growth (Roisin & Pasteels 1987a). This could explain why this species has fewer propensities for attempting to extend its territory at the expense of its neighbors.

The interactions between *M. biroi* and *N. princeps* illustrate a clash between different fighting strategies (Deligne & Pasteels 1982). *M. biroi* uses a static strategy based on its casemate-like nest structure: its nest chambers communicate by small orifices easily obstructed by a soldier's head or walled up by the workers to isolate a damaged or invaded part of the nest ([16]). *N. princeps* uses a movement fighting strategy. The nest and gallery structures of *N. princeps* allow quick troop circulation and easy diffusion of pheromones. The fighting superiority of *N. princeps* over *M. biroi* can be explained by several factors. First, *N. princeps* workers are larger, more powerful and more mobile than those of *M. biroi*, which is important since workers generally play a key role in termite-termite fights (Thorne 1982a). Second, *N. princeps* nests are more voluminous and obviously more populous than *M. biroi* nests. The importance of the numeric advantage in interspecific battles was demonstrated by Jones & Trosset (1991) for two subterranean termites in competition in the Sonoran Desert: the outcome of the battles depended solely on the number of individuals of each species. *N. princeps* may also benefit from the polydomous organization of its colonies: the distance to a nest is reduced in comparison to a monodomous colony and as a consequence, recruitment to battle is faster. Third, there is an efficient short-range coordination between soldiers and workers of *N. princeps*, mediated by the frontal gland secretion (Roisin *et al.* 1990). Yet, despite its superior fighting ability, *N. princeps* seldom displaces *M. biroi* completely, even in plantations more than 40 years old. Several hypotheses might account for this phenomenon. First, *N. princeps* being a poor colonizer by swarming may have difficulties in establishing new colonies in an environment nearly completely monopolized by *M. biroi*. Second, the simple cylindrical coconut trees are not ideal supports for the large *N. princeps* nests. Empty large nests of *N. princeps* fallen on the ground because of their weight were sometimes encountered (Roisin & Pasteels 1986a). Such events should slow down the growth of *N. princeps* populations. Third, whereas a single tree might provide enough resources for a colony of *M. biroi*, large colonies of *N. princeps* may need high food density which is only available in dense habitats.

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[16] for more details see appendix **9**

In ant mosaics, the identity of the dominant species depends to some extent on fluctuations of habitat characteristics, climatic conditions and presence of competitors (Greenslade 1971; Majer 1976a, 1993; Jackson 1984). Substantial changes in community composition may occur naturally within a few years' time (Brown 1959b, Greenslade 1971), or be experimentally induced by the selective removal of a given species (Majer 1976a). Although the dynamics of the mangrove termite communities mapped by Levings and Adams (1984) is not known, their study suggests that the territories occupied by *Nasutitermes corniger* and *N. nigriceps* are relatively constant, as they widely depend on connections between trees and may be stabilized by the elimination of incipient colonies. The present long term study of the interspecific relations among arboreal termites in New Guinean coconut plantations however reveals that important variations in community structure can occur over a period of a few years, and emphasizes the role of competition in the shaping of this structure.

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3. Environmental influences on the arboreal nesting termite community in New Guinean coconut plantations

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M. Leponce, Y. Roisin and J.M. Pasteels

King Léopold III Biological Station, Laing Island, Papua New Guinea, contribution n° 312.

Abstract

Three species of arboreal nesting termites are common in New Guinean coconut plantations: *M. biroi*, *N. princeps* and *N. novarumhebridarum*. Previous studies showed that these three species are in competition with each other. The aim of the present work was to evaluate the influence of environmental factors on this community. We compared the arboreal nesting termite distribution, abundance and colony size in three types of coconut plantation: (i) open plantations with tall trees (~ 25 m) at low density (≤ 100 trees/ha); (ii) standard plantations with medium size trees (~ 13 m) at standard density (100-180 trees/ha); (iii) dense plantations (180 - 300 trees/ha) with medium size or mixed size trees (13-25 m). The overall proportion of coconut trees occupied by arboreal termites increased from 25% in open plantations to 56% in standard or dense plantations. *M. biroi* was less abundant in open plantations than in standard or dense ones, whereas *N. princeps* was scarcest in standard plantations. *N. novarum-hebridarum* occupied about 2% of the trees in all plantation types, but showed a clear preference for dead trees. Nest volumes of all species and colony territories were larger in dense plantations, especially for *N. princeps*. Data on nest thermoregulation suggest that *M. biroi* is the most affected by sun exposure, which could constitute a limiting factor in open plantations. *N. princeps* incipient colonies would be particularly hindered by competition with first established colonies of *M. biroi* in standard plantations. Large territories of *N. princeps* in dense plantations suggest that this species is especially favored by high tree densities, allowing easy colony expansion by galleries or satellite nests and reproduction by budding.

We propose that arboreal termite community structure is mainly shaped by microclimatic conditions and food availability in open plantations, and by interspecific competition in denser habitats, although the incidence of other factors, such as predation or intraspecific competition, remains to be studied.

KEY WORDS Isoptera, *Microcerotermes*, *Nasutitermes*, interspecific competition, nest temperature, nest orientation.

Introduction

The three common arboreal nesting termites in New Guinean coconut plantations, *Microcerotermes biroi* (Desneux), *Nasutitermes princeps* (Desneux) and *Nasutitermes novarumhebridarum* (N. & K. Holmgren), occupy exclusive territories forming a mosaic reminiscent of those observed in ants. They use identical nesting sites –coconut tree trunks– and have similar food habits, consuming dead cellulosic material on the coconut tree or on the ground (e.g. palm leaves, inflorescences, etc.) (appendix **2**). The three species commonly occur side by side in New Guinean coconut plantations, despite their apparent ecological similarity and clear evidence for interspecific competition. We have previously suggested that different reproductive strategies could account for the coexistence of *M. biroi* and *N. princeps*. Whereas the former species seem to be more successful at starting new colonies by independent dealate founders, the latter possesses more mobile soldiers and more powerful workers, and is able to develop populous colonies that extend to a large area, to build satellite nests and often to displace established colonies of *M. biroi* (chapter **2**). Like *M. biroi*, *N. novarumhebridarum* relies on alates to colonize new sites, but seems preferentially associated with dead coconut trees (Roisin & Pasteels 1987a).

Besides reproductive strategies, differential responses to variations of habitat structure and climatic factors can also play an important role in shaping arboreal communities of termites and ants. In arboreal *Nasutitermes*, Adams & Levings (1987) demonstrated that the mosaic of territories of *Nasutitermes nigriceps* and *N. corniger* was affected by the identity of the dominant mangrove tree. In *Rhizophora mangle* mangroves, trees are highly connected and allow the extension of *Nasutitermes* territories. In other mangrove types, trees are not connected and territorial area is limited by tidal flooding. In mosaics of ant species, habitat characteristics and climatic conditions are known to affect the identity of the dominant species. In a long-term study in Solomon Islands coconut plantations, Greenslade (1971) suggested that displacements in ant dominance ranking order were associated with the density of ground vegetation, where some species find a microhabitat particularly propitious in terms of food and humidity. In Ghana cocoa farms, the ant mosaic is subject to seasonal variations associated with the dry season leaf fall, which temporarily renders the habitat unfavorable for the dominant leaf nesting species, *Oecophylla longinoda* and *Tetramorium* (formerly *Macromischoides*) *aculeatum* (Majer 1976a).

Explaining the distribution of arboreal nesting termites in New Guinean coconut plantations and the dynamics of this community requires a good knowledge of the biology of each species, of the way the species interact with each other, and of their responses to environmental changes. In previous articles, we characterized the reproductive biology of the two *Nasutitermes* species (Roisin & Pasteels 1985a, 1986a, 1987a), and presented evidence for territoriality and competition with *M. biroi* (chapter **2**). In this study, we attempted to evaluate the influence of the environment on the arboreal termite community in New Guinean coconut plantations. We first studied how community composition varied among three types of plantations characterized by different tree pattern, height and density, because these properties are likely to determine microclimatic conditions as well as resource availability. Second, we assessed how each species of arboreal termite was affected by environmental factors such as sun exposure and individual tree characteristics (height, health condition, presence of raintracks, inclination).

Materials and methods

Plantation types.

Three plantation types were distinguished on the basis of tree density, plantation pattern and height:

Open plantations: plantations of tall trees (25-30 m in height), widely spaced (10 by 10 m, square plantation pattern), established on the coastal zone of New Guinea by German planters around 1907 (De Silva 1989). Tree density is lower than 100 trees/ha and sunlight is high in this habitat.

Standard plantations: plantations of medium size trees (approximately 13 m) at a density between 100 and 180 trees/ha; trees are generally 8 m to 9 m distant from each other and planted according to a square or triangular pattern (D.P.I. 1975). These plantations were mainly established between World War II and 1975. This habitat is more shaded than open plantations because trees are smaller and more densely planted.

Dense plantations: plantations established by smallholders who planted trees at high density or interplanted new trees between the old ones established by German planters; as a result, the tree height may range from 13 to 25 meters and trees of various height are often mixed. Density is between 180 and 300 trees/ha. This habitat is well shaded.

Coconut trees used in plantations were tall varieties and did not change until the late 1970's when hybrid and dwarf varieties were introduced. Our observations were conducted only in plantations with ages of more than 30 years. Our plantation typology was consistent with differences in ground vegetation. In open plantations the grasses *Pennisetum macrostachyum* (Brongn.) Trin., *Imperata cylindrica* (L.) P. Beauv., *Chloris barbata* Sw. and the sensitive, *Mimosa pudica* L., were dominant. The same plant association was found in standard plantations but the sensitive was less abundant. In dense plantations a fern, *Christella arida* (Don.) Brownsey & Jermy, and an unidentified Fabaceae were the most widespread species.

Study sites.

Study sites were located along the north coast of Papua New Guinea in Madang Province. Climate at this location is tropical humid, with a wet season from November to April and a dry season from May to October (Gressitt 1982). Temperature is fairly constant throughout the year with an average of 28.7°C and extremes of 22 and 34°C, relative humidity is at a minimum at noon (annual average 79%) and at a maximum at night (annual average 97%) (Bouillon *et al.* 1986).

Table 4: Characteristics of plots where termites were sampled.

Plots characteristics

Plot	Plantation	Area (ha)	Plantation type	Random choice ?	Density (trees/ha)
I	Bogia #2	1.0	open	yes	67
II	Danip #1	1.0	open	yes	77
III	Mugil #1	1.0	open	yes	82
IV	Nagada #2	1.0	open	yes	86
V	Bogia #8	1.0	open	yes	99
VI	Nubia #2	1.0	standard	yes	114
VII	Awar #4	0.7	standard	yes	136
VIII	Nubia #3	1.0	standard	yes	136
IX	Potsdam #3	1.0	standard	yes	115
X	Awar #5	0.8	standard	yes	147
XI	Bogia #7	1.0	dense	yes	206
XII	Bogia #5	1.0	dense	yes	215
XIII	Potsdam #2	0.9	dense	yes	224
XIV	Bogia #4	1.0	dense	yes	259
XV	Potsdam #4	1.0	dense	yes	267
XVI	Awar #2a	3.1	standard	no	118
XVII	Awar #2b	0.6	standard	no	144
XVIII	Awar #7	1.0	standard	no	148
XIX	Bogia #1	0.8	open	yes	96
XX	Bogia #6	1.0	dense	no	202
XXI	Bogia #3	1.0	open	yes	91
XXII	Bunu #1	1.0	dense, gaps	no	168
XXIII	Nagada #3	1.0	standard	no	166
XXIV	Potsdam #1a	1.1	dense	no	259
XXV	Potsdam #1b	0.8	dense	no	225
XXVI	Siar #1	1.0	dead trees	no	75
XXVII	Siar #2	1.0	see text	yes	124
XXVIII	Vidar #1	1.0	see text	yes	91
XXIX	Potsdam #5	1.1	cocoa/coconut	no	241

Twenty-nine quadrats were mapped between September 1990 and April 1994 (Table 4). Within each quadrat, trees were numbered with acrylic paint. Every tree was inspected and the presence of termites or ants was recorded, nest size and distance to the ground were measured (or when the nest was out of reach, estimated using a clinometer Suunto PM-5/1520). Nest orientation was measured from the nest center with a sight compass, to the nearest five degrees. Tree condition (healthy, burnt, stump, ...) was also noted.

Plots I-XV were randomly selected among coconut monocultures and represented 5 replicates per plantation type. Sites with big gaps, sites invaded by arboreal nesting ants, and sites with an unusual plantation structure were excluded from this series to minimize the effect of environmental parameters other than plantation structure. These plots thus correspond to standardized habitat conditions. Plots XVI-XXV also fitted into the plantation types recognized above. They were either randomly selected plots excluded from the first series because they did not match all the standardized conditions, or plots selected non-randomly to study inter- or intraspecific relationships. Plots

XXVI-XXIX were selected for specific studies. Plot XXVI was composed of 93% of dead trees, which had been killed by the planters for agricultural purposes 10 years before this study. Plot XXVII was composed of tall trees planted at standard density. Plot XXVIII was like plot XXVII, but with big gaps. Plot XXIX was a dense plantation of coconut intercropped with cocoa, where an unusual number of coconut trees were inclined.

Nest volumes.

Nest volumes were computed using an algorithm appropriate to nest shape: sector of a hollow cylinder for *M. biroi* and ellipsoid for *N. princeps* and *N. novarumhebridarum* (see appendix **1**). Nest volume was used as an indicator of nest population size because a good correlation was found between these two factors in the arboreal neotropical species *Nasutitermes corniger* and *N. ephratae* (Thorne 1985a). Finding two (or even three nests) on the same tree was common in *M. biroi* and rare in both *Nasutitermes* species. In such cases, because the nests were always connected to each other as part of a single colony, their individual volumes were pooled as though they constituted a single nest.

Territory mapping.

Nests and galleries were mapped in all quadrats. Sympatric *Nasutitermes* colonies were always distant enough to be unambiguously delineated on maps. In *M. biroi* this was only possible in open plantations. To infer *M. biroi* colony extension in a standard plantation (plot VI), we relied on agonism between colonies (as previously described for *N. princeps* in Roisin *et al.* 1987) and on the presence or absence of reproductives in the nests, assuming that there is only one nest containing reproductives per colony. This method was too laborious to be repeated in other plots.

Climatic conditions in plantations.

A meteorological cabinet containing a thermohygrograph (Lambrecht KG Göttingen type 252 Ua or Jules Richard type NG5484) was placed in each of the plantation types to get synchronous recordings of air temperature and humidity in these microhabitats. Recordings were made from March to July 1993.

Nest microclimate.

Microclimate in nests was measured in 1993 with two thermohygrometers fitted with a temperature/humidity probe (Hanna HI 8564 and Acez) and in 1994 with a Solomat MPM4000 environment recorder equipped with two thermometer probes (Pt 100 and thermocouple). One of the probes was inserted in a PVC pipe (diameter: 2.54 cm) introduced straight into the middle of the nest and as possible to the tree trunk. To avoid recording an artificial elevation of temperature caused by termites that usually crowd around any new object inserted into their nest (Grassé & Noirot 1958), the PVC pipe was inserted into the nest at least one week before installing the probe. The top end of the PVC pipe was sealed with silicone to avoid air exchanges with the outside of the nest. Another probe was put just under the nest surface, on the vertical plane of symmetry of the nest, to reveal when and how much direct sunlight was heating the nest. On some occasions the second probe was put in a meteorological cabinet to measure the external air temperature. Temperature recordings started 24h after installing the probes. Four nests of *M. biroi* and four nests of *N. princeps* were studied. One nest of *M. biroi* was killed with ethyl acetate and Baygon to compare nest temperatures in the presence and absence of living termites. No measurements were conducted on *N. novarumhebridarum* because its nest structure is fairly similar to that of *N. princeps*.

Tree inclination, orientation of raintracks.

Tree inclination was measured with a plumb line and a protractor. The direction towards which trees were leaning was measured with a compass. The extent and orientation of "raintracks" (i.e., humid trunk sectors where mosses and algae are found) on the trees were measured with a tape measure and a compass.

Statistical analyses.

Arcsine transformations were performed before conducting analyses of variance (ANOVA) on proportions (Zar 1984). Orientation of termite nests was analyzed by methods for circular distributions (Batschelet 1981, Zar 1984).

Results

Termite communities in relation with plantation type

Proportion of trees occupied by termites.

The proportion of coconut trees occupied by arboreal nesting termites varied significantly with plantation type (plots I-XV one-way ANOVA on transformed data: $F=14.082$; df=2, 12; $P<0.001$) (Figure 17). The average proportion of trees occupied in open plantations (25%)

was significantly lower than in standard plantations (58%) (Tukey test for multiple comparison of means: P<0.001) or in dense plantations (54%) (Tukey: P<0.01). Standard and dense plantations did not show a significant difference (Tukey: P= 0.811).

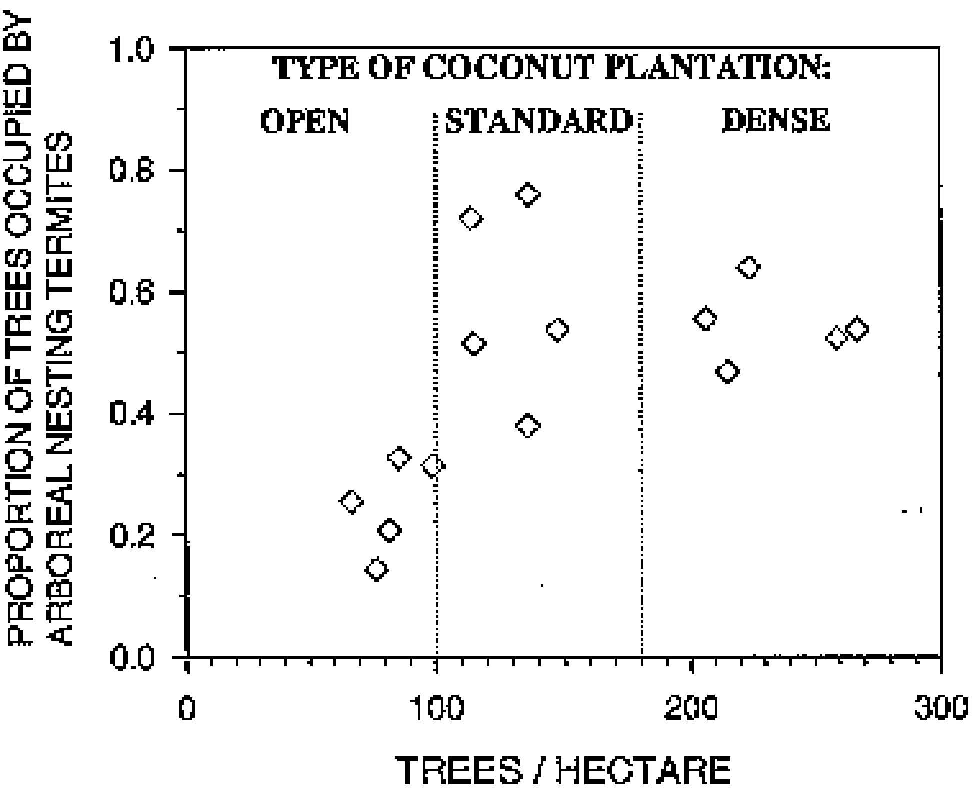

Figure 17: Proportion of trees occupied by arboreal nesting termites in plots I to XV corresponding to the 3 plantation types.

The proportion of coconut trees occupied by nests or galleries of *M. biroi* differed among plantation types (one-way ANOVA: F=20.269; df=2, 12; P<0.001) (Figure 18). *M. biroi* occupied a smaller proportion of the trees in open plantations (mean = 16%) than in standard (m= 56%; Tukey: P<0.001) or dense ones (m= 43%; Tukey: P<0.01). A significant difference among plantation types also appeared with *N. princeps* (one-way ANOVA: F=8.782; df=2, 12; P<0.01), occupying fewer trees in standard plantations (m=1%) than in dense ones (m= 9%; Tukey: P=0.04). The difference between standard and open plantations (m=5%) was of borderline statistical significance (Tukey: P=0.051). No significant difference among plantation types was found in the average proportion of trees occupied by *N. novarumhebridarum* (m= 2.0%; one-way ANOVA: F=1.420; df=2, 12; P= 0.280).

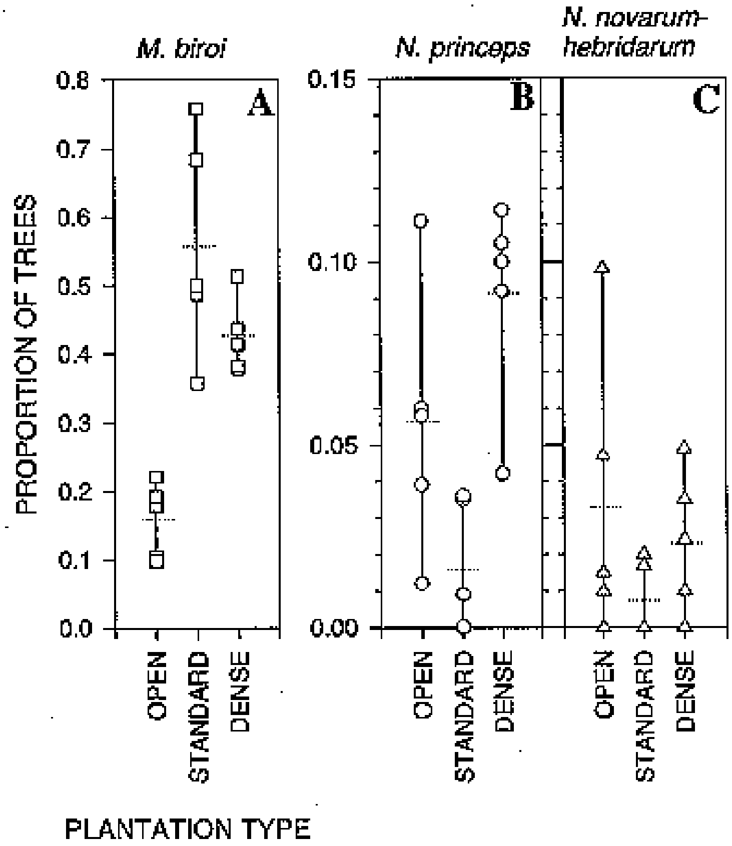

Figure 18: Proportion of trees occupied by (A) *M. biroi*, (B) *N. princeps* and (C) *N. novarumhebridarum* in the three plantation types. Hollow symbols represent observed values, dotted lines represent averages.

Nest volumes.

Nest volumes of *M. biroi* (Fig. 19) varied significantly among plantation types (plots I - XV, one-way ANOVA: F=7.762; df=2, 740; P<0.01). Average nest volume per tree in open plantations (mean ± standard deviation=9.1± 6.7 liters, n=49) was not significantly different from that observed in standard plantations (m=10.8 ± 9.2 liters, n= 267) (Tukey: P=0.577) but was smaller than in dense plantations (m=13.5 ± 11.6 liters, n= 427) (Tukey: P<0.05).

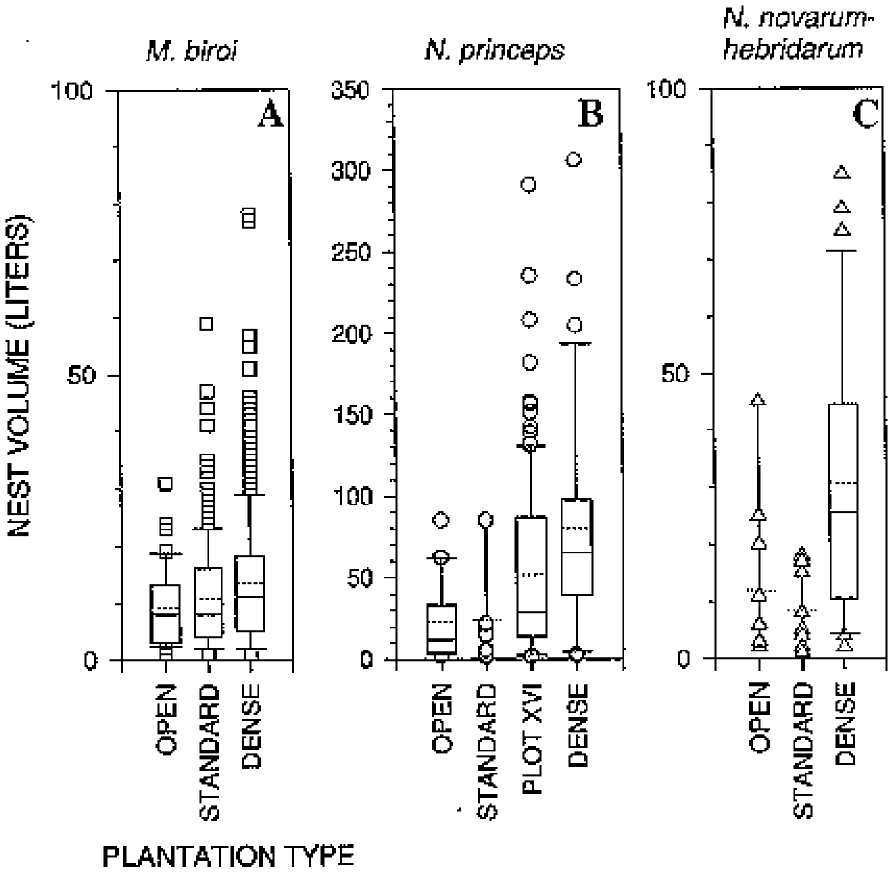

Figure 19: Distribution of nests volumes for *M. biroi* (A, data from plots I-XV), *N. princeps* (B, plots I-XV & XVII-XXV, presumed unicolonial nests of plot XVI) and *N. novarumhebridarum* (C, plots I-XXV) in the three plantation types. Box plots were used when more than 15 values were available, otherwise all observed values were plotted. The horizontal lines inside the boxes represent the median (solid line) and the average (dotted line). The horizontal ends of the boxes represent the quartiles. The fences are defined as 10% and 90% percentiles. Values outside the fences are represented by individuals symbols.

Nasutitermes nests being less abundant than nests of *M. biroi*, data from plots XVI-XXV were added to those from plots I-XV to obtain a sufficient sample size. The results should therefore be considered with some caution because they might be affected by other causes than plantation structure. For *N. princeps*, results from plot XVI were treated separately because all nests from this site probably belonged in an unicolonial system (chapter **2** and chapter **5**); furthermore, this plot enclosed a small patch of secondary growth which may have modified the availability of food. Nest volumes of *N. princeps* varied significantly among plantation types (plots I-XV and XVII-XXV, one-way ANOVA: F=7.839; df=2, 62; P<0.01). Average nest volume in dense plantations (m=80.2 ± 67.7 liters, n=39) was significantly larger than in open (m=23.2 ± 25.2 liters, n=16, Tukey: P<0.01) or standard plantations (m=25.9 ± 32.9 liters, n=10, Tukey: P<0.05). In plot XVI, the average nest volume was 51.8 ± 55.1 liters (n=134), a value significantly lower than the one obtained in dense plantations

(Tukey: P<0.05) but not significantly different from the one observed in open plantations (Tukey P=0.203) or in standard plantations (Tukey P=0.480).

An analysis of variance of *N. novarumhebridarum* nest volumes among the three plantation types led to the same conclusions as for *N. princeps* (plots I-XXV, one-way ANOVA: F=5.547; df=2, 43; P<0.01): average nest volumes did not differ between open plantations (m=12.1 ± 14.1 liters, n=10) and standard ones (m=8.8 ± 6.9 liters, n=8, Tukey: P=0.934), but were significantly larger in dense plantations (m=30.7 ± 23.7 liters, n=28, Tukey: P<0.05).

Territory area.

Colonies of *M. biroi* generally occupied one to three trees in open plantations (plots I-V) and in standard plot VI. In the other standard plots and in dense plantations, their area was not investigated. Colonies of *N. princeps* had a markedly greater area in dense plantations than in open or standard ones. In dense plantations, the total number of trees occupied by a colony was 4-20 (plots XI-XV, m>10.5, n=9 colonies; the precise mean could not be calculated, some occupied trees being out of the mapped area) and the most remote tree was situated 15-88 m (m=31.7m) from the nest. In open or standard plantations (plots I-X), a colony occupied 2-4 trees (m=2.6), the most remote of which was situated 5-39 m (m=14.8m) from the nest (n=8 colonies). *N. novarumhebridarum* colonies also tended to occupy more trees in dense plantations (plots XI-XV: 2-6 trees, m=3.6, n=11 colonies) than in open or standard ones (plots I-X: 1-3 trees, m=1.8, n= 6 colonies).

Vertical nest distribution.

The distance from the ground to the base of each nest was measured in plots I-XXV. In *M. biroi*, the vertical nest distribution was not different among plantation types (Kolmogorov-Smirnov tests P>0.05). The nest base was below 0.7m in 25% of the nests, below 1.1 m in 50%, below 2.0 m in 75% and below 4.5 m in 90% (n=1140). For both *Nasutitermes* species, data from each plantation type, insufficient to perform a comparison, were pooled. The 25th, 50th, 75th and 90th percentiles of *N. princeps* nest distribution were respectively 1.0, 1.3, 2.2 and 3.3 m (n=234). In *N. novarumhebridarum*, values of 0.5, 0.8, 2.4 and 6.0 m (n=36) were obtained for the same parameters.

Nest orientation.

Distribution of nest orientation was not uniform. The prevailing *M. biroi* nest orientation was north-east (Fig. 20) but mean angles were significantly different among plantation types (plots I-XXV, Watson-Williams test for circular distributions: F=3.571; df= 2, 1143; P<0.05): 41° ±

92° (mean angle ± circular standard deviation, mean vector lenght ρ_l = 0.28) in open plantations (n=71); 16° ± 94° in standard plantations (n=574, ρ_l = 0.26); 29° ± 81° in dense plantations (n=501, ρ_l = 0.37). Although the sample size was much smaller, nests of *N. princeps* also showed a prevailing north-east orientation (Fig. 20), with mean angles significantly different among plantation types (Watson-Williams test, F=3.427, df= 2, 204; P<0.05): 41° ± 64° in open plantations (n=22, ρ_l = 0.51); 0° ± 90° in standard plantations (n=153, ρ_l = 0.29); 28° ± 64° in dense plantations (n=29, ρ_l = 0.54). Regarding *N. novarum-hebridarum*, too few data were available to perform a statistical analysis on nest orientation.

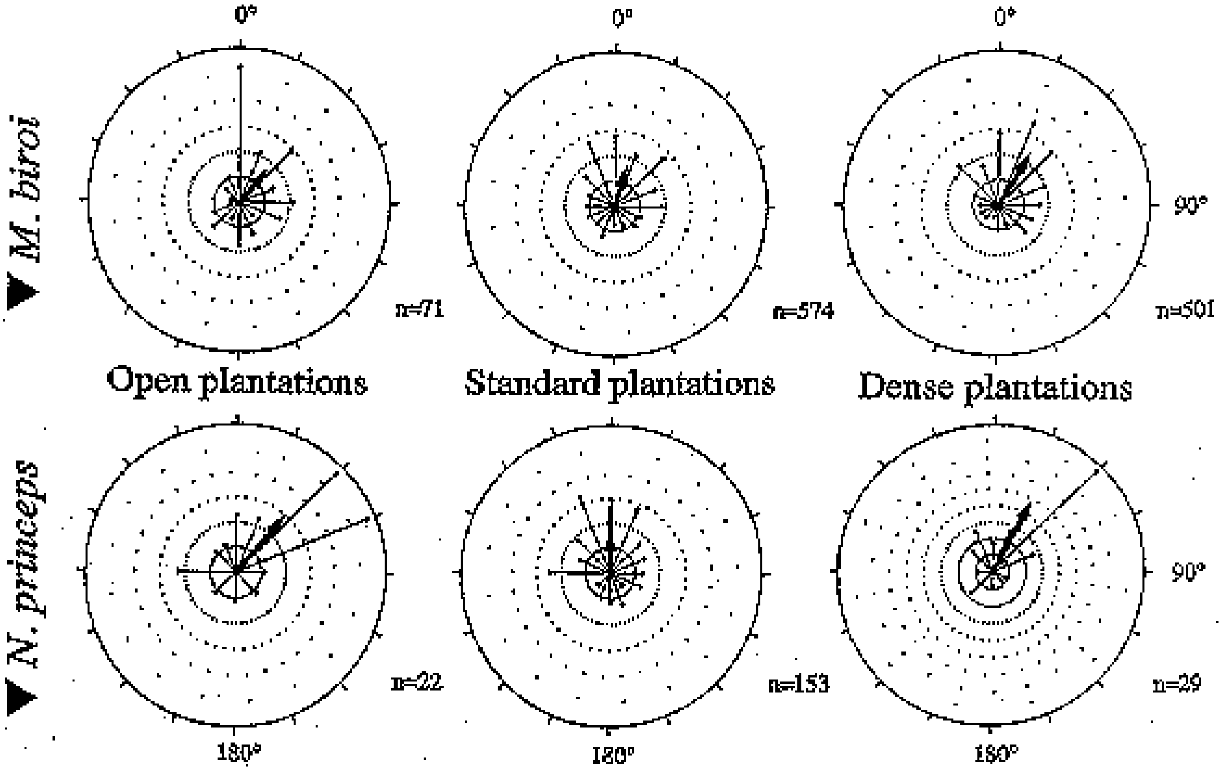

Figure 20: Circular histograms for orientation of *M. biroi* nests and *N. princeps* nests in the three plantation types. Magnetic north= 0°, east= 90°, etc. True north lies about 6° east of magnetic north. Each concentric circle represents a frequency increment of 4%. Arrows represents the mean vector which may range from 0 (no mean direction) to 1 (all nests concentrated at the same direction).

Effect of environmental variables on termites

Temperature and humidity.

Air temperature and humidity in the shade were measured in the three plantation types. Because differences were small, we will only compare here open and dense plantations. From March to July 1993, temperature fluctuated between 22 and 33°C. Daytime temperature was generally 1°C higher in open plantations but night temperature was identical in both habitats. The maximum difference observed between the two plantation types was 3°C. Relative humidity was approximately the same in both habitats. During daytime, relative humidity was inversely related to temperature and was seldom lower than 70%. At night and during rains, relative humidity reached saturation.

Figure 21 shows temperature variations under the surface and in the core of a nest of *M. biroi* (Fig. 21A) and a nest of *N. princeps* (Fig. 21B) in comparable conditions: both nests had the same north-east orientation and were surveyed in open plot I in April 1994. The surface temperature of both nests increased abruptly from 7 AM, because they were exposed to direct sunlight, to reach a maximum around 10 AM. The surface temperature then slowly decreased. Temperature records of other nests showed that surface temperature can reach 50°C in both species. Figure 21 also reveals that the relationship between nest surface and core temperature is markedly different between the two species. In *M. biroi*, core temperature followed

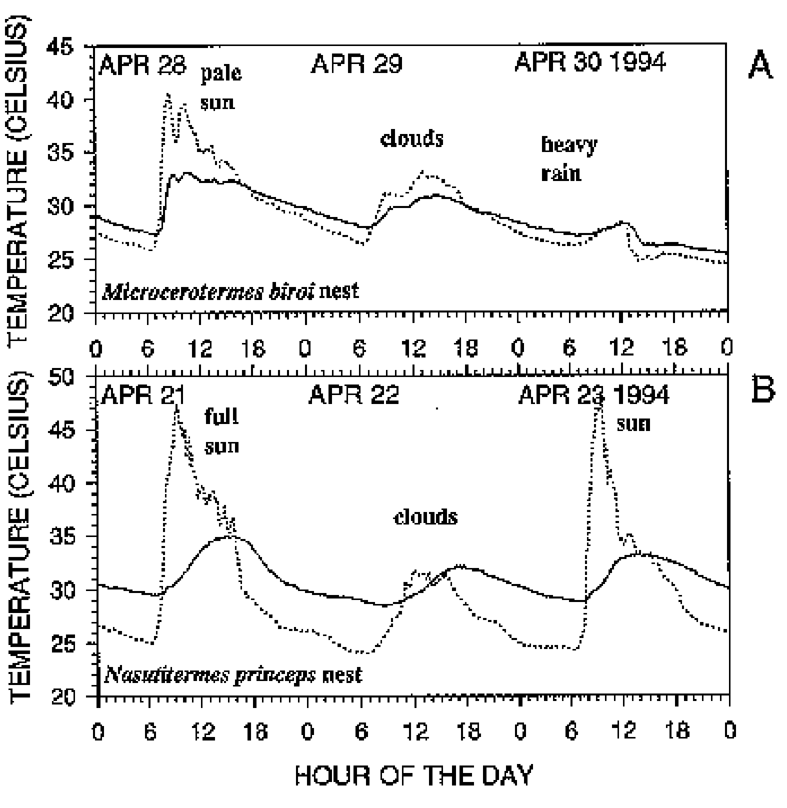

Figure 21: Temperature variation recorded every 10 minutes at the center (solid line) and under the surface (dotted line) of north-easterly oriented nests of *M. biroi* (A), orientation: 50°, and *N. princeps* (B), orientation: 55°.

almost exactly ups and downs of surface temperature, though with a lower amplitude. In *N. princeps*, core temperature varied in a much delayed and smoothened way. Actually, core temperature rose when the surface was warmer than the core, and fell when it was cooler. Records from shaded nests showed that the average core temperature of *N. princeps* (29.0-31.6°C, the higher figure corresponding to the larger nests) was slightly higher than that of *M. biroi* (28.5°C), which was almost equal to the average external air temperature (28.7°C). Temperature variations were similar in a nest of *M. biroi* before and after its inhabitants were killed: live nest temperature range, May 12-14, 1993, was 27.5-31.1°C, with an external air temperature of 24.2 -29.6°C; dead nest temperature, June 22-24, 1993, ranged between 27.2-29.3°C, with an external air temperature of 25.2-32.2°C. Relative humidity in the core of two *M. biroi* nests ranged from 91 to 99%. In a nest of *N. princeps*, relative humidity ranged between 98 and 100%.

Tree height.

The energy expenditure required to reach the food sources in the tree crown (dead palms and inflorescences) and to build covered galleries leading to them vary with the tree height. We investigated whether tree height alone could account for differences in termite distribution observed between plantation types, because trees are tall (~ 25 m) in open plantations, smaller (~13 m) in standard ones and of variable size in dense ones.

Plot XXVII, with a plantation pattern similar to standard plantations but with tall trees had a global occupation by termites of 42.9% (*M. biroi* 35.2%, *N. princeps* 7.7%, *N. novarumhebridarum* absent), thus in the range observed in standard plantations (plots VI-X: 38-76%). In plot XXVIII, similar to plot XXVII but with big gaps, only 29.0% of the trees were occupied by arboreal termites (*M. biroi* 21.7%, *N. princeps* 6.5%, *N. novarumhebridarum* 0.8%), a value close to the average for open plantations (24.8%).

In dense plantations of medium and tall trees (plots XI, XII, XIV, XV), occupation by arboreal termites was very similar on the 867 tall (*M. biroi* 37.9%, *N. princeps* 9.5%, *N. novarumhebridarum* 4.7%, total 52.2%) and on the 617 medium size trees (*M. biroi* 39.3%, *N. princeps* 7.6%, *N. novarumhebridarum* 5.1%, total 52.0%).

Tree condition.

Dead trees still standing up, lying on the ground, or reduced to stumps represented on average 3.2% of trees in plantations (all plots except XXVI, where trees had been deliberately killed). Dead trees were as likely to be occupied by termites as live ones (Cochran corrected χ^2 = 2.029 , df=1, P> 0.05), but not by the same termite species (χ^2= 61.597, df=2, P<0.001): the occurrence of *N. novarumhebridarum* was almost four times as frequent on dead trees as on live ones (12.7% vs 3.2%), and the abundance of this species relative to all arboreal termites reached 24.2% on dead trees, versus 6.8% on live ones (Table 5).

Table 5: Occupation of trees by termite nests and galleries (n) or termite galleries only (g) and tree condition (alive or dead) (data from plots I to XXVIII).

Tree condition	Termite species				Total
	M. biroi	*N. princeps*	*N. novarumhebridarum*	no termites	
alive	1617 (946 n + 671 g)	527 (158n + 369g)	156 (71 n + 85 g)	2531	4831
dead	52 (17 n + 35 g)	39 (10 n + 29 g)	29 (8 n + 21 g)	108	228
Total	1669	566	185	2639	5059
% on dead trees	3.1%	6.9%	15.7%	4.1%	4.5%

Raintracks.

Trees may display more humid sectors, covered with algae and bryophytes, which we called “raintracks”. Raintracks were found more often in dense plantations. In plot XIV, raintracks covered the whole circumference of the trunk in 30 trees. In the other trees with raintracks, raintracks covered an average sector of 94° ± 60° of the circumference (n=93, range: 10°-282°, orientation: 6° ± 65°, mean vector lenght ρ_1 = 0.53). Presence of *M. biroi* nests was independent from the presence of a raintrack in plots XIV and XXIV (Cochran corrected χ^2 = 0.194, df=1, P>0.05) but, when a raintrack was present, nests were in 32/39 (82%) cases built outside the raintrack. In plot XIV, on trees with a raintrack, *M. biroi* covered galleries were built in 71/78 (91%) cases in both dry and wet sectors and in 7 cases they were only built in the dry sector of the tree. Response of the two *Nasutitermes* species to the presence of raintracks was not studied.

Tree inclination.

The tree inclination was suspected to influence the termite nest orientation and the relation between these two factors was studied in *M. biroi*. In plot XXIX, 80% of the coconut trees were inclined and 48% supported a *M. biroi* nest. A positive angular correlation (r =0.55) between the direction in which a tree was leaning and the orientation of the nest it supported was found in that plot. On the other hand, in the surroundings of plot XIV, where 63% of the trees were inclined and 17% supported a *M. biroi* nest, the angular correlation between tree inclination and nest orientation was much lower (r=0.10). In both plots the average tree inclination was about 8°.

Discussion

Overall termite abundance varied with plantation density: on average, 25% of the trees were occupied in open plantations versus 56% in standard or dense plantations. *M. biroi* occupied fewer trees in open plantations, but the abundance of *N. princeps* was lowest in standard plantations. *N. novarumhebridarum* occupied a small percentage of the trees in all plantation types, and showed a significant preference for dead trees. Average nest volume of all species was higher in dense plantations than in open or standard ones. The average area occupied by a colony of *N. princeps*, and to a lesser extent, of *N. novarumhebridarum*, was also larger in dense plantations. The current study suggests that two environmental factors may be of special importance for the abundance and extension of arboreal termite colonies: sun exposure and density of available resources.

Air temperature and humidity vary little between plantation types and are unlikely to influence arboreal termite distribution. However, direct sunlight has profound, species-specific effects on nest temperature. In nests of *M. biroi*, the fact that the core temperature closely follows variations of surface temperature reveals rapid transfers of heat through such nests. The termites themselves seem to play no role in nest thermoregulation, because their presence or absence does not influence temperature variations. The nests of *M. biroi* thus show poor insulating capacities. This agrees with the results of Lüscher (1961), who observed that the temperature within an arboreal nest of *Microcerotermes edentatus* rose and fell with the outside temperature. The tolerance of *M. biroi* to high temperatures is not known, but temperatures of 40 to 50°C under the nest surface are very high for a termite. Mitchell *et al.* (1993) demonstrated that the critical thermal maximum of *Hodotermes mossambicus*, a termite living in arid areas, ranged between 43.5 and 48.5°C. Collins *et al.* (1973) established that *Gnathamitermes perplexus*, another desert-living termite, had an outstanding temperature tolerance and foraged between 9°C and 49°C. The temperature near the core of termite nests generally ranges between 25°C and 35°C, with uppermost values of 38°C (Bristow & Holt 1987; Greaves 1964; Holdaway & Gay 1948; Josens 1971; Lüscher 1961; Malaka 1977; Watson & Abbey 1986). The fact that the temperature sometimes reached 35°C in the core of *M. biroi* nests, and increased steeply toward the nest surface, suggests that sun exposure might actually constitute a limiting factor for *M. biroi* in open plantations. Comparing Figs 5A and 5B reveals that an abrupt rise of the surface temperature is followed by a much slower increase of the core temperature in *N. princeps* than in *M. biroi*. The cores warms up or cools down slowly, depending on the temperature gradient between the core and the surface. Shaded *N. princeps* nests maintain a core temperature higher than the external air temperature, probably by retaining metabolic heat generated by the aggregated termites (Peakin & Josens 1978; Watson & Abbey 1986; Holdaway & Gay 1948; Greaves 1964), metabolic heat which is probably dissipated in poorly insulated *M. biroi* nests. Although no microclimatic data were collected from nests of *N. novarumhebridarum*, it is likely that their thermoregulatory capacities are close to those of *N. princeps*, because both species have nests of similar shape and structure.

The density of dead palm leaves, which constitute the main food source for *M. biroi* and *N. princeps*, should be proportional to the density of trees. However, in open plantations, part of these food items are often unattractive to termites because they are dessicated by sunlight. By contrast, as tree density increases, food items on the ground are better protected from dessication by the shade of living palms, by the ground vegetation and by other food items as they pile up on a limited space. Food availability thus probably increases more than linearly with habitat density. In addition, a higher tree density facilitates the establishment of connexions between neighboring trees. Because a single tree is sufficient to sustain a colony of *M. biroi*, the lower abundance of this species in open plantations can hardly be explained by resource limitation. By contrast, because the colonization strategy of *N. princeps* largely depends on colony expansion and the production of new nests by budding (Roisin & Pasteels 1985a, 1986a, Roisin 1987), this species should be especially favored by high tree densities. Our observations were consistent with the following hypotheses: in both species, nest volumes, likely to be good estimators of colony size (Thorne 1985a), increased with tree density. In addition, the extension of *N. princeps* colonies was significantly higher in dense plantations. Regarding *N. novarumhebridarum*, Szent-Ivany (1956) already noticed that this species was often present on trees hit by shells during the war or by lightnings. In New

Guinean coconut plantations, casual observations also suggested that this species might prefer dead trees (Roisin & Pasteels 1987a). This fact is now well established, because *N. novarumhebridarum* was almost 4 times more abundant on dead trees than on live ones. This preference explains why this species constitutes a constantly small proportion of the arboreal termite community in all plantation types. Although *N. novarumhebridarum* also feeds on dead palm leaves or other debris, the larger volume of its nests and the larger area of its territories in dense plantations can be explained as for *N. princeps*.

With borderline statistical significance, the abundance of *N. princeps* in standard plantations tended to be lower than in open or dense ones, but remained highly variable. Whereas *N. princeps* was absent from two of the randomly selected standard plots (VII and VIII), plot XVI, also of standard density, was remarkable for its dense, probably unicolonial population of *N. princeps*. Further sampling would be necessary to determine to what extent the observed scarcity of *N. princeps* in standard plantations is ecologically meaningful or the result of random variations in species distribution. Neither climate nor food availability could explain why standard plantations should be less favorable for *N. princeps* than open ones. However, a possible reason for scarcity of *N. princeps* in standard plantations could be interspecific competition (see chapter 2). Because *M. biroi*, which seems to be a pioneer species, is more abundant in standard than in open plantations, the establishment of *N. princeps* colonies in standard plantations could be generally hindered. However, once a colony of *N. princeps* has managed to become established and populous enough to displace neighboring colonies of *M. biroi*, the abundance of *N. princeps* could rise dramatically, as in plot XVI.

No difference in the vertical distribution of nests was found between the three species, nor between plantation types in *M. biroi*. By contrast, a pattern of nest orientation was found in *M. biroi* and *N. princeps*. Preferential nest orientation is a phenomenon known in some mound building *Amitermes* (Gay & Calaby 1970, Grigg 1973, Grigg & Underwood 1977, Jacklyn 1991), *Drepanotermes perniger* (Watson & Perry 1981), *Tumulitermes hastilis* (Hill 1942) and ants (e.g., *Solenopsis invicta*: Hubbard & Cunningham 1977) and is interpreted as favoring thermoregulation. For example, north-south orientation of wedge-shaped mounds of *Amitermes laurensis* prevents excessive heating by presenting a low profile to the midday sun (Grigg 1973, Jacklyn 1992). In New Guinean coconut plantations, just south of the equator, the north side of tree trunks is more exposed to sunlight than the south side during the dry season. However, at all times of the year, oblique sunlight coming from the east in the morning or from the west in the afternoon is as likely to increase the temperature of arboreal nests as near-zenithal midday sun, which hits nests at a lower angle and which is cut off by the tree crown. Actually, steep increases in the surface temperature of sun-exposed and north-easterly orientated nests of *M. biroi* and *N. princeps* were observed as the sun rose, and maxima were reached well before noon. In addition, the orientation of *M. biroi* and *N. princeps* nests is far more variable than the orientation of so-called "magnetic" termite mounds: the circular standard deviation around the mean orientation ranges between 60° and 90° for both species versus 8-9° in *Amitermes laurensis* (calculated from the data of Grigg & Underwood 1977). Finally, a significant difference in mean nest orientation was also observed between the three plantation types, and even nests in the shade presented a prevailing orientation. For all these reasons, we cannot establish whether avoidance of excessive sun exposure has any influence on the nest orientation in *M. biroi* and *N. princeps*. Avoidance of excessive humidity could also have some importance, as suggested by the tendency, shown by *M. biroi*, to build nests outside of raintracks. Tree inclination was not consistently correlated to nest position. The mechanism responsible for nest orientation thus remains a largely unanswered question.

We have previously suggested that differences in colony dispersal strategies allows the coexistence of *N. princeps* with *M. biroi*, whereas *N. novarumhebridarum* would differ from the other species by exploiting preferentially dead trees (Roisin & Pasteels 1987a; chapter 3). We are now able to refine this hypothesis. In open plantations, the overall density of arboreal colonies is relatively low. The colonization by *M. biroi* is likely to be limited by climatic conditions, the spread of *N. princeps* colonies by tree and food density. In these conditions, interspecific interactions would be of secondary importance. Standard and dense plantations are more favorable for the colonization by *M. biroi*, but also for the development and expansion of large colonies of *N. princeps*. In denser habitats, overall termite density is higher and interspecific competition fiercer. Our observations suggest that *N. princeps* colonies may have difficulties getting established, especially in plantations of standard density, but once they reach a critical size, they could expand and displace *M. biroi*. However, several other factors may also limit the spread of either species; for instance, intraspecific competition could hinder the expansion of single colonies, whereas invasions by ants or other enemies could bias the interspecific relations. The role of such factors is still to be investigated. The association between *N. novarumhebridarum* and dead trees supports the hypothesis that this species, which relies exclusively on dispersal flights for colony multiplication, is particularly able to colonize such massive but widely spaced resources and to secure their exploitation (Roisin & Pasteels 1987a).

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4. Reproductive mechanisms and dynamics of habitat colonization in *Microcerotermes biroi* (Isoptera: Termitidae)

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M. Leponce, Y. Roisin and J. M. Pasteels

Contribution No. 320 from King Léopold III Biological Station, Laing Island, Papua New Guinea.

Abstract.

1. Previous studies on the arboreal termite community in coconut plantations of northern New Guinea showed that *Microcerotermes biroi* is the most abundant species, despite the fighting superiority of two competitor species *Nasutitermes princeps* and *N. novarum-hebridarum*. In this study we tested the hypothesis that the success of *M. biroi* is due to its efficiency at colonizing new habitats following nuptial flights.
2. We demonstrated experimentally the ability of *M. biroi* colonies to replace their reproductives when removed, or to produce reproductives in satellite nests when isolated from the remainder of the colony. Replacement reproductives were always neotenics, derived from nymphs or workers.
3. Despite the ability of neotenics to differentiate within their home colonies, 84% of field colonies were headed by dealated imagos, this value constitutes a minimum estimate of the proportion of field colonies founded independently by imagos after the nuptial flight.
4. The monitoring of a young plantation during the first 3½ years of its colonization by arboreal nesting termites revealed its invasion by *M. biroi*, which colonized 63% of the trees while neither *Nasutitermes* species appeared.
5. Our results demonstrate that *M. biroi* is actually a pioneer species, able to invade a new habitat by means of nuptial flights. They outline the importance of each species' reproductive strategy in shaping the arboreal-nesting termite community.

Key words. Reproduction, dispersal, arboreal-nesting termites, Papua New Guinea.

Introduction

In northern New Guinea coconut plantations, the arboreal-nesting termite community comprises three species, which exclude each other from the trees: *Microcerotermes biroi* (Desneux), *Nasutitermes princeps* (Desneux) and *N. novarumhebridarum* (N. and K. Holmgren). *M. biroi* is the most common species in the habitat despite the aggressive superiority of the two *Nasutitermes* species, especially of *N. princeps* which often invades neighboring *M. biroi* nests during the expansion of its territory. *N. novarumhebridarum* interferes less than *N. princeps* with *M. biroi* because it is less abundant in the habitat and occupies smaller territories. In a previous study (chapter **2**), we proposed that interspecific differences in reproductive strategies might be one of the major factors explaining the observed community structure. Whereas *N. novarumhebridarum* spreads by nuptial flights and preferentially occupies dead trees (Roisin & Pasteels, 1987a; chapter **3**), *N. princeps* is apparently a poor long-range colonizer which relies more on budding (i.e., the establishment of satellite nests followed by the development of reproductives within them) for colony propagation (Roisin & Pasteels, 1986a; Roisin, 1987). The fact that *M. biroi* is the most common species in the habitat, although its nests are subject to invasion by the competitor species *N. princeps* and *N. novarumhebridarum*, suggests that *M. biroi* is a pioneer species especially good at colonizing available habitats. If so, this species should rely mostly on nuptial flights for dispersal, since such flights are more efficient than budding at achieving long-range colonization. The aim of this study was to evaluate these two hypotheses: the reliance of *M. biroi* on nuptial flights and its ability to colonize a new habitat.

In termites, the mode of formation of a colony can often be inferred from the type and number of reproductives found in it. When imagos found a colony after the nuptial flight, they remain as fully pigmented individuals with well-cut wing scales (remnants of their shed wings). Usually a single pair of founders is present, although in some species colonies are founded by multiple alates (pleometrose) (Weyer, 1930b; Thorne, 1984; Darlington, 1985c, 1988; Roisin, 1993). If reproductives differentiate in their colony of origin, either to replace the founders after their death or in a satellite nest during a budding process, they may arise from alates (adultoids), nymphs (nymphoid neotenics) or workers (ergatoid neotenics) (Noirot, 1956). Nymphoids and ergatoids are generally present in large numbers: they lack wing scales and resemble the caste they come from apart from being more darkly pigmented. Nymphoids have compounds eyes and wing buds, absent in ergatoids. Adultoids are usually indistinguishable from primary reproductives, but they are sometimes less pigmented, show imperfectly cut wings or, as in *N. princeps*, nanitic features such as smaller eyes, narrower pronotum or shorter wing scales (microimagos, Roisin & Pasteels, 1985a). Like nymphoids and ergatoids, adultoids are generally present in large numbers, although the differentiation of a single pair of adultoids was repeatedly observed in orphaned colonies of *Nasutitermes coxipoensis* (Lefeuve, 1987). In all forms of reproductives, females differ from males by the enlargement of the 7th sternites (genital plate) and often show distinctive abdominal swelling (physogastry).

The capacity of each caste to differentiate into replacement reproductives may vary greatly between species, even within a genus. In *Microcerotermes* species, nymphoids and ergatoids have been commonly observed (Weyer, 1930a; Noirot, 1956; Roisin, 1990), whereas adultoids were only reported in *M. parvus* (Noirot 1956, 1985). In the genus *Nasutitermes*, adultoids were found in species such as *N. polygynus* (Roisin & Pasteels, 1986c), *N. corniger* (Thorne, 1982c; Roisin & Pasteels, 1986c), *N. princeps* (Roisin & Pasteels, 1986a,b), *N. coxipoensis* (Lefeuve, 1987) whereas other species, such as *N. novarumhebridarum*, rely exclusively on ergatoids (Roisin & Pasteels, 1987a).

In order to determine the mode of formation of colonies in coconut plantations, we first tested the physiological ability of *M. biroi* to produce replacement reproductives after the removal of the sexuals from a nest or after the isolation of a satellite nest from its parent nest. Secondly, we compared the type and number of reproductives obtained by these experiments with those found in field colonies, to evaluate the relative importance of nuptial flights and budding in the onset of new colonies under natural conditions. Finally, in order to test whether *M. biroi* would actually prevail over other arboreal termites such as *Nasutitermes* species during the colonization of a new habitat, the development of arboreal termite colonies was monitored for 3½ years in a plot of 100 young trees from which they were initially absent.

Material and methods

This study was conducted in Awar, Nubia and Potsdam coconut plantations in Bogia District, Madang Province, on the north coast of New Guinea. The climate at this location is tropical humid (Gressitt, 1982) with a wet season from November to April and a dry season from May to October.

Differentiation of replacement reproductives

The ability of *M. biroi* to produce replacement reproductives was tested by orphaning experiments and by budding experiments:

In orphaning experiments, the reproductives were removed from 26 nests, of which 21 contained a physogastric imaginal queen and 5 contained male and female nymphoid neotenics. The royal cell was first located by cutting the lateral edges of the nest with a machete and looking for the presence of the nursery (i.e., the nest portion where eggs and young larvae are concentrated) which is always situated nearby. The royal cell was then detached from the trunk in one piece and carefully opened. Twenty-one nests containing a physogastric imaginal queen were used for three sets of experiments: (1) removal of the imaginal royal pair (in 2 nests) (2) removal of the queen only while the imaginal king was put back into the royal cell or, when missed during nest dissection, assumed still to be around the royal cell (in 12 nests) (3) removal of the imaginal king only while the queen was put back into the royal cell (in 7 nests). In these three sets of experiments, the royal cell was sealed with adhesive tape and nailed back to its original location. In nests containing neotenics, the royal cell and a large area around it were removed in the hope of having collected all reproductives. The reproductives, together with a sample of the nest population, were fixed in FAA (formaldehyde : alcohol : acetic acid, in the proportion 70 : 25 :5) and preserved in 70% ethanol. Most orphaning experiments were conducted during the wet season, in March 1993, and a few others during the dry season, in July 1993. All nests were reexamined in March-April 1994, and a new sample of the nest population, including replacement reproductives if present, was collected.

In budding experiments, all nests with reproductives (26 nests) were entirely removed from a one-hectare quadrat (A7, 148 trees), leaving 29 satellite nests, to test if replacement reproductives would develop within them. Nests with an empty royal cell, satellite nests with a low population, or that were severely damaged during nest examination, were also removed (15 nests). Two situations were distinguished: satellite nests on trees supporting the parent nest (15 occurrences) and satellite nests on trees not supporting the parent nest (14 occurrences). Parent nests were removed at the end of June 1993 and satellite nests were re-examined at the end of March 1994. Samples were collected from all satellite nests as in orphaning experiments.

Reproductives in field colonies

The frequency of the different reproductive forms (imaginal pair, neotenics) was assessed from a sample of 136 nests coming from two one-hectare quadrats, N2 and A7, and from adjacent plantations. In N2 and A7 all nests were systematically dissected, in April 1992 and June 1993 respectively. Plot N2 had been previously mapped in September 1990 so that all young nests (less than 19 months old) could be unambiguously identified at the time of nest dissection. A sample of each nest population was collected and reproductives were later identified and counted under a stereoscopic microscope.

Dynamics of colonization and colony growth

Dynamics of colonization of a virgin habitat was studied in A3, a young coconut plantation (100 trees on 0.70 ha) established in 1982. This young plantation was adjacent to plantations established for more than 40 years and occupied by *M. biroi*, *N. princeps* and *N. novarumhebridarum*. This plot was mapped in September 1990 and in April of years 1992, 1993 and 1994. Nest dimensions were measured at the time of mapping to calculate nest volume and estimate colony growth from one year to the next. As a *M. biroi* colony is sometimes polydomous (composed of multiple nests), all individual nest volumes on a single tree were pooled to depict colony size.

Results

Differentiation of replacement reproductives.

When parent nests were orphaned, imaginal reproductives were always found in a single chamber royal cell whereas nymphoid reproductives were located in a multichamber royal cell. The old single chamber royal cell, nailed back to its original location after the removal of the reproductives, was never reused. Nymphs, absent from nests orphaned in March 1993 at the end of the wet season (except in 2 nests where only 1 individual was present in the sample), were present in most nests sampled in June-July 1993, during the dry season.

When nests were re-examined several months after orphaning, replacement reproductives were found in 12 out of 21 nests (57%) from which imagos were removed, and in all 5 nests from which nymphoids were removed (table 6, nests #1-21 & 22-26). In March 1994, out-of-season nymphs of various instars and of both sexes were found in all the 17 orphaned nests in which a replacement took place. Replacement reproductives were nymphoid neotenics and, in a few cases, ergatoid neotenics. The number of nymphoids found 12 months after orphaning was highly variable and ranged from 1 young female nymphoid in nest #2 to 317 nymphoids of various ages in nest #10. The primary queen or king put back into its royal cell never survived the manipulation. Replacement of primary reproductives was significantly more successful in experiments where the queen was removed than in experiments where the queen was put back (table 6, nests #1-14 vs. 15-21) (Pearson Chi-Square= 8.964, df= 1, P< 0.01).

Table 6: Results of orphaning experiments: caste composition (sexual line) in nests from which reproductives were removed in March 1993 (except colonies marked with *: October 1993 and **: July 1993). All nests re-examined in March-April 1994. Numbers of replacement reproductives in the sample should be considered as indicative since some sexuals might have been missed during dissection of the nest.

	initial caste composition:		final caste composition:			
nest #	nymph instars 0 = absence	alates	nymph instars	alates	nymphoids	ergatoids
I. Primary queen and king removed, royal cell put back.						
1	0	no	2-4	no	36	2
2	0	no	1-4	no	1	0
II. Primary queen removed, king left or not found, royal cell put back						
3	0	no	1-4	no	24	0
4	0	no	2-5	no	180	0
5	0	no	2-5	no	201	0
6	0	no	4	no	46	0
7	0	no	3-5	yes	71	0
8	0	no	1-5	no	151	49
9	0	no	3-5	no	140	0
10	2 (1 indiv.)	no	1-5	no	317	10
11*	0	yes	1-4	no	>170	>17
12	0	no	?	no replacement reproductives		
13,14	0	no	dead			
III. Primary king removed, queen left, royal cell put back						
15**	4-5	no	1-4	no	145	0
16,17,18	0	no	?	no replacement reproductives		
19,20,21	0	no	dead			
IV. Nymphoid queens and kings removed, royal cell removed						
22	2 (1 indiv.)	no	4, 5	no	27	1
23**	1-4	no	3, 4	no	13	0
24**	1-5	no	1, 3-5	no	47	0
25**	4, 5	yes	2,4,5	no	8	2
26**	3-4	yes	1-5	no	34	0

Experimental removal of all parent nests in site A7 induced the differentiation of secondary reproductives in 55% (16/29) of the satellite nests left (table 7). Replacement was significantly more frequent in satellite nests when the removed parent nest was initially on the same tree than when it was not (11/15 nests (73%) vs. 5/14 (36%); table 7, nests #41-55 vs. 27-40; Pearson Chi-Square= 4.144, df= 1, P< 0.05) whereas death of nests occurred at the same rate in both situations (4/15 and 4/14 nests). Replacement reproductives were predominantly nymphoids, but ergatoids were also found always with nymphoids. Out-of-season nymphs of both sexes were present in all nests with neotenics at the time of re-examination (March 1994), as well as in 3 of 5 nests lacking neotenics.

Table 7: Evolution of caste composition in satellite nests after the complete removal of their parent nests in June-July 1993. All nests were re-examined end of March 1994.

		initial caste composition:			final caste composition:			
nest #		nymph instars	alates		nymph instars	alates	nymphoids	ergatoids
I. Satellite nests which were not on the same tree as their parent nest.								
27		4	no		3 - 4	no	>180	25
28		4	no		3	no	77	36
29		3, 4	no		1- 4	no	79	59
30		?	no		3 - 4	no	47	2
31		?	no		1- 4	no	26	0
32-36		3 - 5	in 2 nests		in 3 nests:	no	no replacement reproductives	
					4 -5			
37-40		3 - 5	no		dead			
II. Satellite nests which were on the same tree as their parent nest.								
41		?	no		2, 3	no	21	4
42		2-5	no		3-5	no	19	0
43		0	no		3,4	no	24	0
44		3-5	no		2-5	no	15	0
45		3,4	no		3-5	no	10	0
46		3,4	no		1-5	yes	6	1
47		4	no		2-4	no	13	3
48		3,4	no		2-5	no	3	0
49		4	no		1-5	no	145	9
50		4	no		2-4	no	13	0
51		3, 4	no		4 (1 indiv)	no	100	4
52-55		3, 4	no		dead			

Adultoid replacement reproductives were never obtained, even in the nests that contained alates at the time of reproductive removal (nests #11, 25, 26, 32, 33). Instead, numerous nymphoid queens and kings were present in 3 of the 5 nests dissected whereas the other two did not contain any secondary reproductives at all.

Reproductives in field colonies

In two one-hectare quadrats in mature plantations (N2 and A7), all nests and galleries were mapped and nests were systematically dissected (Fig. 22). The number of colonies on 1 ha was similar in N2 (29 nests with reproductives) and A7 (26 nests with reproductives). *M. biroi* nests were found on 41% of the trees present, and their foraging galleries reached an additional 20% of the trees. Trees with a single nest were most frequently observed (66% of the nest supporting trees), however two (27%) or even three nests (7%) were sometimes encountered on a single tree. On approximately half (53%) the trees supporting one or several *M. biroi* nests, one nest contained a royal cell occupied by reproductives. Two nests with royal cells were twice found on a single tree (2% of the trees supporting *M. biroi* nests) but, in each case, only one of them contained reproductives (a pair of imagoes). A single tree thus never supported more than one colony. Trees supporting nests with an empty royal cell (13% of the trees supporting *M. biroi* nests) or without any royal cell (32%) were also present. Between September 1990 and April 1992, 15 new nests appeared and 7 nests died in N2. Among the 15 young nests, 9 were found with a royal cell either containing a pair of imagos (7 occurrences) or empty. Other new nests were apparently satellite nests since they had no royal cell. Two of the nests that died were observed invaded by ants before they perished..

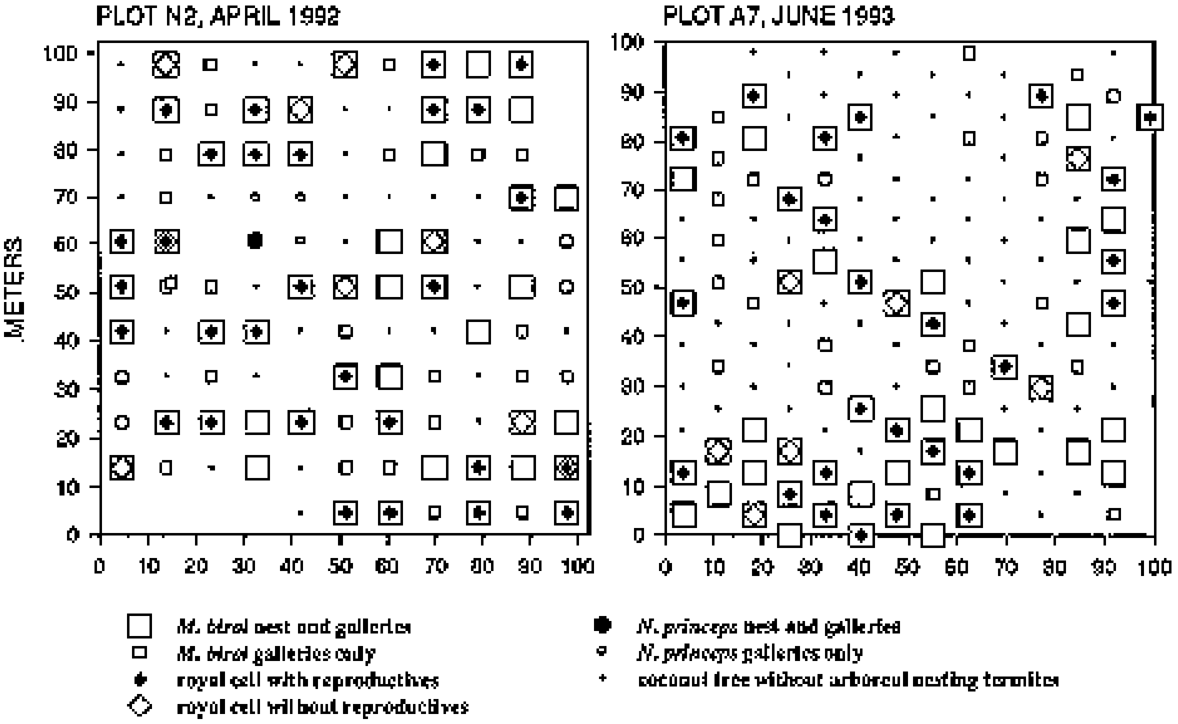

Figure 22: Maps of one-hectare plots N2 and A7, showing the distribution of nests with royal cell and reproductives, of nests without reproductives, and of carton-covered galleries of *M. biroi* and of *N. princeps*.

Taking into account all nests dissected during this study, it appears that a pair of imagos (a king and a physogastric queen) was present in 107/136 (79%) of the nests containing reproductives. In another 7 nests (5%), imagos and nymphoid reproductives were found together in a single royal cell. Three of these nests were found with a pair of imagos and supplementary reproductives (Table 8: nests #56-58, Fig. 23), the other four nests contained 1 imago and 1 to 6 nymphoid replacement reproductives of the opposite sex (Table 8: nests

#59-62). Nymphoid neotenics in the absence of imagos were present in 22 (16%) of the colonies examined. Ergatoid neotenics were never observed in any of the field colonies examined here.

Table 8: Composition of nests found with both imaginal and secondary reproductives (Q: queens, K: kings).

nest #	date	imagos	nymphoids
56	8-Jul-93	1Q + 1 K	1 K
57	10-Mar-93	1Q + 1 K	1 K
58	10-Mar-93	1Q + 1 K	3 Q
59	13-Apr-92	1K	3Q
60	13-Apr-92	1Q	1K
61	1-Jul-93	1 Q	1 K
62	1-Jul-93	1 Q	6 K

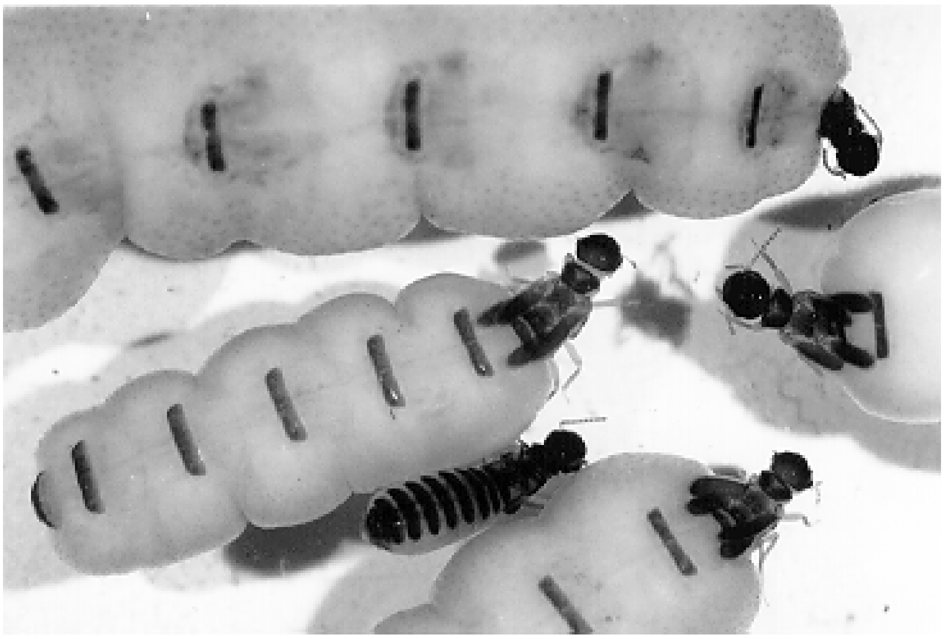

Figure 23: Three supplementary nymphoid queens found together with 1 imaginal queen (at the top) and 1 imaginal king in nest #58, 10 March 1993.

Colonization of a young plantation and colony growth

Site A3 was completely devoid of arboreal nesting termites in September 1990. The first *M. biroi* colonies occupied 10% of the trees in April 1992; two years later, *M. biroi* occupied 63% of the trees present (Fig. 24). Of the 8 nests observed in A3 as early as 1992, one died but the other 7 reached in less than 3½ years volumes over 11 liters (maximum: 55 liters), the average *M. biroi* nest volume (chapter **2**). Nests that appeared later, and which were one or two years old in 1994, reached an average volume of 5 liters (n=34) when less than 1 year old and increased on average by 13 (n=19) the second year. Remarkably, not a single occurrence of any other arboreal nesting termite was recorded in plot A3 during this study, despite the fact that *N. princeps* and *N. novarumhebridarum* were present in adjacent mature plantations.

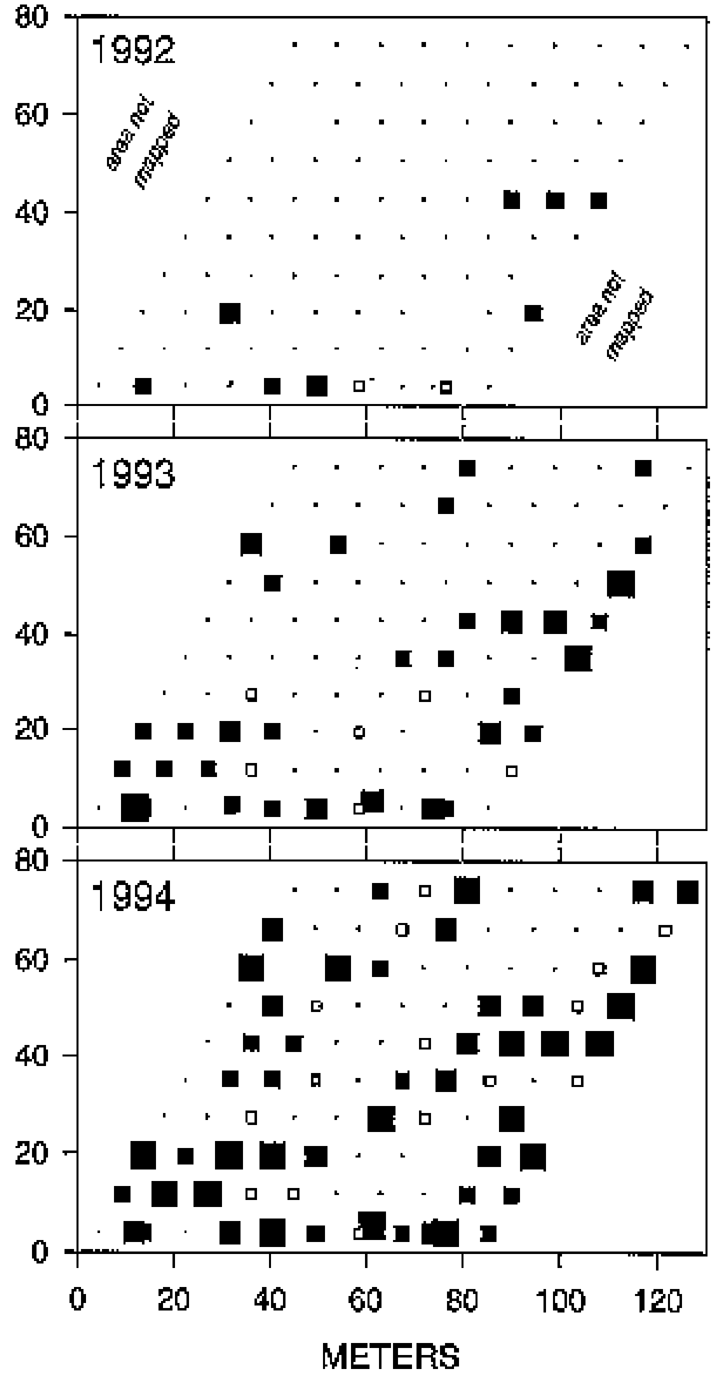

Figure 24: Colonization by *M. biroi* of young coconut plantation A3. Filled squares= trees with *M. biroi* nests and galleries, hollow squares= trees with *M. biroi* galleries only, dots= coconut trees without arboreal-nesting termites, area without dots was a part of the young plantation which was not surveyed

Discussion

Reproductive replacement in *M. biroi* follows a pattern common to many Termitidae (Noirot, 1985) and already observed in other *Microcerotermes* species such as *M. amboinensis* (Weyer, 1930a), *M. parvus* (Noirot, 1956) and *M. papuanus* (Roisin, 1990): replacement reproductives arise from nymphs or temporarily from workers. Nymphs are normally present only during the dry season and workers develop into neotenics probably to compensate for the deficit of reproductives. Ergatoids are apparently superseded afterwards, probably once egg production by nymphoids, which are more fertile than ergatoids (Noirot 1955; Roisin, 1990), reaches a sufficient level. As observed in other species (Roisin, 1990; Lenz *et al.*, 1988; Lenz & Runko, 1993) out-of- season nymphs were present in nests headed by neotenics. The adaptive value of this phenomenon is open to speculation. One possibility is that such nymphs initially appeared as neotenic candidates, potentially involved in the replacement process. Another possibility is that these nymphs constitute an immediately increased investment in alates which could perpetuate the gene pool of the colony in case of failure of the replacement process (Lenz & Runko, 1993). In our experiments, 11 of 14 orphaned colonies (79%) regained reproductives after the removal of their primary queen. In nests from which only the primary king was removed, it is likely that the primary queen, which finally died, delayed the appearance of replacement reproductives, as Sieber (1985) observed in *Macrotermes michaelseni*. The percentage of recovery from orphaning under natural conditions is expected to be higher than that observed here, with nests under sudden and intense stress due to manipulation. Budding is potentially possible in *M. biroi* since replacement reproductives differentiated in satellite nests once the influence of their parent nest was cut off. For unknown reasons, satellite nests were more likely to experience the differentiation of replacement reproductives if they were originally on the same tree as their parent nest than if they were not. Whether the reproductive potentialities of the individuals inhabiting a satellite nest actually differ according to its remoteness from the parent nest remains to be investigated.

Unlike *M. parvus* (Noirot, 1956), adultoid replacement reproductives were never observed in *M. biroi* even in those nests containing alates at the time of orphaning. When imagos are found heading a field colony, they can thus be identified as the ones that founded this colony after accomplishing the nuptial flight. In coconut plantations, a large majority (84%) of the colonies therefore result from independent foundations of this kind. This figure constitutes a minimum estimate, since the finding on nymphoid neotenics does not exclude the possibility that the colony was founded by independent dealates, which died and were replaced by nymphoids. In *M. biroi*, imagos were always found as a single pair but the possibility of colony initiation by multiple queens and kings and the subsequent reduction to one pair before colony maturity can not be excluded: pleometrosis was observed in the closely related species, *M. amboinensis*, by Weyer (1930b). Nymphoids together with a royal primary pair were found in 2% of *M. biroi* colonies. Such assemblages of reproductives were also noticed in *M. amboinensis* (Weyer, 1930a) but in this case, the nymphoids involved were non-functional. The presence of 3 physogastric nymphoid queens in one of the dissected *M. biroi* nests suggests that such supplementary nymphoids are at least sometimes functional in *M. biroi*. Unilateral replacement of either the primary queen or the primary king occurred in 3% of *M. biroi* colonies, which were found with a limited number of replacement reproductives. Associations solely composed of nymphoids occurred in 16% of the colonies, among which some are probably buds while the others result from the replacement of an imaginal, primary pair. Consequently, budding, also suspected by Weyer (1930a) in *M. amboinensis*, is probably a marginal way for *M. biroi* to propagate its colonies. Despite good abilities to replace its primary reproductives, only a low proportion of *M. biroi* colonies contained neotenics, which suggests either that primaries are long lived or that the causes leading to the death of the primary reproductives generally destroy the whole colony. With the exception of the invasion of *M. biroi* nests by *Nasutitermes* species (chapter **2**), major causes of death of entire colonies such as diseases, predators or abiotic factors are poorly documented. Predation by ants is one of the most likely causes of death of *M. biroi* colonies: of 50 nests in plot N2, 7 were partly or completely invaded by ants and among them 4 had an empty royal cell.

An empty royal cell was observed in 13% of the trees supporting *M. biroi* nests in plots N2 and A7. The empty royal cell always had a single chamber, indicating the death of primary reproductives rather than of neotenics, and was sometimes reshaped with smaller cells inside the large flat royal chamber, suggesting that the nest might have been taken over by a colony that was not its original builder. Intraspecific competition was evidenced by the fact that two *M. biroi* colonies were never observed on a single tree. The occurrence of actual attacks by conspecific colonies was never witnessed and remains uncertain. Nest takeover could also occur without aggression if a nest is already dead when discovered by foragers of a neighbor colony.

The ability of *M. biroi* to colonize a new habitat rapidly was well demonstrated in site A3, where 63% of the trees were colonized by *M. biroi* in less than 3½ years. This level of occupation of trees was similar to the one observed in older plantations such as N2 or A7, and many nests had grown above the average size. *M. biroi* was the only arboreal nesting termite species which appeared in A3, which shows that *M. biroi* is the first species to colonize the habitat.

Even though all species can be expected to channel a substantial part of their resources into dispersing forms, even in relatively stable habitats (Hamilton & May 1977), the arboreal nesting termites of New Guinea coconut plantations broadly differ in their reproductive investment strategy. *M. biroi* appears effectively as a pioneer species which colonizes the habitat by means of nuptial flights. *M. biroi* invades the habitat with many relatively small, monogynous colonies. Its main competitor *N. princeps* exhibits an opposite strategy with a tendency to build large, often polygynous colonies which propagate by budding, and can invade and kill nests of *M. biroi* during the expansion of their territory. Like *M. biroi*, *N. novarumhebridarum* is monogynous and reproduces by nuptial flights (Roisin & Pasteels, 1987a) but is not widespread in this habitat, probably because of its attraction to dead trees (chapter **3**). This resource is scarce and dispersed in mature coconut plantations, and of course even scarcer in young plantations. Reproductive strategies thus appear as one of the main factor shaping the arboreal nesting termite community in coconut plantations.

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5. Intraspecific interactions in a community of arboreal nesting termites

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M. Leponce, Y. Roisin and J.M. Pasteels

King Léopold III Biological Station, Laing Island, Papua New Guinea, contribution n° 322.

Abstract

1. In coconut plantations of northern New Guinea, the arboreal nesting termite community comprises three species: *Nasutitermes princeps*, *N. novarumhebridarum* and *Microcerotermes biroi*. In order to assess the importance of intraspecific interactions in this community, we conducted pairwise encounters between batches of individuals in the laboratory and between entire nest populations in semi-natural conditions.
2. Three levels of agonism were defined in laboratory bioassays: anagonism, moderate agonism and strong agonism. Anagonism was observed during all control tests with homocolonial groups and in some tests with allocolonial groups of all species. Moderate agonism included initial aggressiveness that subsequently faded out, and initially passive encounters where aggression progressively built up and led to fighting. Strong agonism corresponded to initial aggressiveness and fighting.
3. Results obtained in laboratory bioassays were consistent with bioassays in semi-natural conditions. When *Nasutitermes* colonies were anagonists in laboratory bioassays, their foraging trails merged without aggression in field tests. *N. princeps* nests that were moderately agonistic in laboratory tests fought and either continued to avoid each other or finally joined after elimination of the most aggressive individuals. The most aggressive *M. biroi* and *N. princeps* colonies fought and their foraging trails diverged afterwards. Direct attacks on alien nests were witnessed in *M. biroi*.

4. In all species, anagonism occurred in 21-34% of the combinations tested, either between geographically close or distant colonies. An exception was a group of 112 anagonist nests of *N. princeps*, which most probably constituted a supercolony. The level of agonism between *Nasutitermes* colonies was constant during the wet and the dry season.
5. Termite colonies excluded each other, both intra- and interspecifically, from the coconut trees, and their territories seem distributed in a mosaic pattern. Agonism between colonies may result in the elimination of the weakest colonies or in trail divergence, maintaining this mosaic. By contrast, lack of agonism between some colonies suggests the possibility of colony fusion and gene exchanges without nuptial flights.

KEY WORDS: intraspecific competition; territoriality; agonistic behavior; colony fusion; Isoptera, Termitidae.

Introduction

Termite colonies are generally closed to allocolonial conspecifics (reviewed in Thorne & Haverty 1991). Some species maintain territories from which intruders are apparently excluded. Aggressive interactions at the territory boundary of conspecific colonies have been evidenced in the mound building termite *Macrotermes michaelseni* (Darlington 1982b), in the subterranean termite *Heterotermes aureus* (Jones 1993) and in the arboreal nesting termite *Nasutitermes nigriceps* (Levings & Adams 1984). Such intraspecific aggressiveness, often together with interspecific antagonism apparently affects the spatial distribution of colonies: mounds in African and Australian ecosystems are often overdispersed (Wood & Lee 1971; Collins 1981; Lepage 1984; Abe & Darlington 1985; Spain *et al.* 1986; Pomeroy 1989), territories of *Heterotermes aureus* (Jones & Trosset 1991, Jones 1993) and of *Nasutitermes* spp. (Levings & Adams 1984, Adams & Levings 1987) apparently form a mosaic similar to mosaics of territories of dominant ants (review of Majer 1993, Adams 1994a). By contrast, conspecific colonies may also fuse, as observed in *Coptotermes formosanus* by Su & Scheffrahn (1988).

In coconut plantations of the northern New Guinea coastline, the arboreal nesting termite community comprises three species of Termitidae which exclude each other from coconut trees, offering special interest for studies on competition. On average, one hectare of a dense coconut plantation supports 234 trees, 100 of which are occupied by 28 *Microcerotermes biroi* colonies, 21 trees are occupied by 3 *Nasutitermes princeps* colonies, and 6 trees by 2

N. novarumhebridarum colonies (chapter **3** and **4**). In a previous study, we provided evidence for asymmetries between competitive abilities in the 3 species: both *Nasutitermes* were able to destroy *M. biroi* colonies; this ability allowed *N. princeps* to expand its colonies in a habitat preempted by the faster colonizer, *M. biroi* (chapter **2** and **4**). *N. novarumhebridarum*, which apparently prefers dead trees (Roisin & Pasteels 1987a, chapter **3**), has more restricted colonies and interferes less with the two other species. Until now, intraspecific relationships have received little attention except in *N. princeps*, where the existence of agonism between neighbor colonies was previously demonstrated, although lack of agonism sometimes occurred between individuals from different colonies (Roisin *et al.* 1987). Interactions between *M. biroi* colonies are probably frequent because of the high density of colonies in this habitat and also in *N. princeps* since large concentrations of nests are sometimes found. In *N. novarumhebridarum*, allocolonial individuals may also encounter, especially on dead trees. The goals of the present study were to assess the frequency and intensity of intraspecific agonistic interactions between colonies of the three species and to evaluate factors possibly affecting aggressiveness in order to estimate the influence of intraspecific agonism on community structure. To reach these goals, we performed laboratory bioassays between groups of individuals from different colonies (or from the same colony as controls) of each of the three species. Because it is still uncertain whether laboratory bioassays, conducted under highly artificial conditions are representative of natural encounters (Thorne & Haverty 1991), we corroborated and extended the laboratory tests by confronting entire nests on an experimental area in semi-natural conditions. Individuals from the same pairs of nests were confronted in different seasons because a seasonal variation of agonism has been observed in European *Reticulitermes* species (Clément 1986). Agonism among close neighbors (nests from the same site) and nests from distant sites was compared, as the latter are less likely to be genetically closely related and as it has been demonstrated that genetic relatedness affects to some extent allocolonial aggressiveness in another arboreal termite, *Microcerotermes arboreus* (Adams 1991).

Materials and Methods

Study sites

Colonies tested came from coconut plantations spread along a 30 km coastal strip from Bogia to Awar, Madang Province, Papua New Guinea.

Aggression bioassays in laboratory

Termites used in laboratory bioassays were collected by removing a portion of their nest in the field. In all species, pairwise bioassays between neighbors (colonies from a single site) and between non-neighbors (colonies from different sites) were carried out. As controls, trials were also conducted between termites coming from the same colony. Twenty-six nests of *N. princeps* from 4 sites, 18 nests of *N. novarumhebridarum* from 4 sites and 15 nests of *M. biroi* from 5 sites were used in these tests. The experimental groups were composed of soldiers and large workers (in the ratio soldiers:workers 3:17 in *M. biroi* and 1:1 in *N. princeps* and *N. novarumhebridarum*, in order to simulate foraging groups) and placed in plastic Petri dishes 5.5 cm in diameter lined with moist filter paper. Three tests per combination were performed: two replicates in a one-dish arena and one replicate in a three-dish arena. Preliminary and *a posteriori* comparisons of the two experimental set-ups indicated that they yielded the same results. More replicates were performed when dubious results were obtained and some tests were replicated over time (see below). In the one-dish set-up, a group of 20 individuals on an nest fragment from one colony (A in Fig. 25a) was placed into a Petri dish, then confronted with a group of 20 individuals from another colony (B in Fig. 25a) holding to a nest fragment. The three-dish arena was a refined version of the one-dish arena: the number of termites per colony was doubled and the confrontation method was less disruptive. The experimental arena was composed of three Petri dishes glued together in a straight line and communicating by holes 4 mm in diameter (Fig. 25b). During the acclimatization period, both termite groups were confined in their own Petri dish by a plastic cylinder (as in dish containing A, Fig. 25b). At the beginning of the test, these cylinders were removed and the arena covered with a glass slide. Behaviors during encounters were then video recorded under low light (260 lux) for 3 to 30 minutes. The video tapes were reviewed later and allowed more detailed observations of agonistic reactions. A dot of yellow paint on the abdomen distinguished members of one colony from the other. The paint (ICI Dulux exterior gloss acrylic) was water based and dried within 20 minutes at 25°C; our preliminary laboratory tests indicated that it caused no observable mortality or behavioral modification. All assays were performed on the day termites were collected to avoid any effect of prolonged isolation of termites from their home colony and were initiated when termites were quiet and gathered on the fragment of their nest material, generally within less than 3 hours after introduction of the termites. Any manifestation of aggressiveness or lack thereof was noted during the three minutes following the first encounter between allocolonial termites. Five levels of initial aggressiveness were recognized: (1) indifference: no examination, walking at normal speed, forward-and-backward body oscillation; (2) discrimination: prolonged unilateral or mutual antennation, pursuit; (3) threats, nip: bites inflicting no apparent injury; (4) strong alert: jerk back when in contact with alien, increase in locomotory speed, frenetic forward-and-back oscillation; (5) attack: bites that pierce the exoskeleton, emission of defensive secretion (*Nasutitermes* soldiers only), head banging (*M. biroi* soldiers only). Dead or conspicuously wounded workers and soldiers were counted after 24 h. Initial aggressiveness and final mortality were combined to define a level of agonism between the two colonies. Level I, anagonism, and level III, strong agonism, are opposite responses. In level I, no initial aggressiveness was observed; death rate, never due to fighting, was below 10%. In level III, initial aggressiveness (threats, strong alert and attack) or at least evident discrimination always was observed and death rates, due to fighting, were always over 10%. Level II, moderate agonism, covers all intermediate outcomes, i.e., no initial aggressiveness but high delayed mortality, or initial aggressiveness but low mortality (< 10%) and even, in some of the replicates, no evidence of agonistic reactions and of mortality due to fighting. When moderate agonism was detected, additional replicates (up to 15, depending on the availability of material) were generally performed.

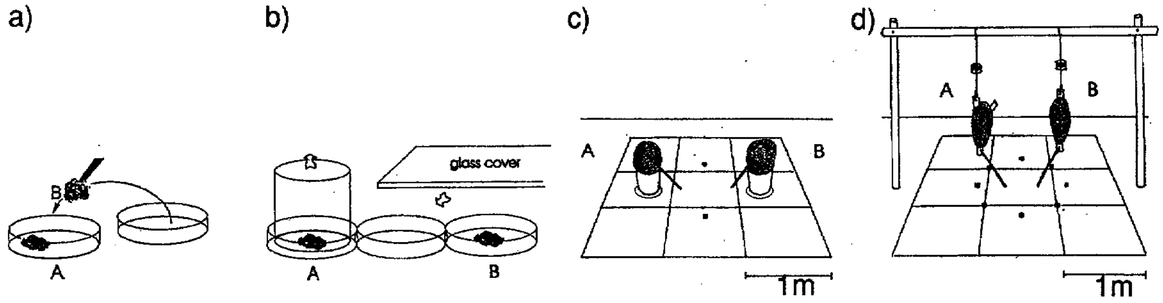

Figure 25: experimental set-ups used in laboratory and field bioassays: a) single Petri dish arena b) three Petri dish arena c) experimental area used to confront the population of two *Nasutitermes* spp. nests placed in plastic containers. d) portico used to confront the population of two *M. biroi* nests hung by ropes and connected to the experimental area with two sticks. For details see text.

Assays involving *N. princeps* and *N. novarumhebridarum* were first conducted in July-August 1991, during the dry season, and repeated during the wet season in February-March 1992. Assays involving *M. biroi* were only conducted during the wet season, in April-May 1992. Additional tests were performed in 1993 and 1994 in order to compare results yielded in the laboratory and in semi-natural conditions (see below).

Aggression bioassays with entire nests in semi-natural conditions

To force encounters between termite colonies, nests were transplanted from the field to experimental areas of 9 m² of cleared ground. A grid of ropes 1 m apart facilitated mapping of foraging trails. Nine of these areas were established on Laing Island in the forest near King Léopold III Biological Station. The experimental set-up was inspired from that used by Thorne (1982a), but was adapted to the nest volumes of the studied species. Experiments involving *N. princeps*, *M. biroi* and *N. novarumhebridarum* colonies were conducted in, respectively, May-June 1993, June-July 1993 and April 1994. Colonies were confronted for at least 4 days and up to 3 weeks. A sample of the nests population was collected prior to test initiation and at the end of the experimental period.

Entire *Nasutitermes* nests with a volume ranging from 60 to 100 liters were collected in the field by removing them from the tree trunk and placing them directly in a large plastic container (garbage bin) which was then brought to Laing Island. Containers were arranged on the experimental area which comprised two wood baits 1.4 m apart (Fig. 25c). Each container, from which termites could not escape, contained a small amount of dead wood and moist paper. Ants were prevented from entering the nest by a water barrier. Two days of acclimatization allowed the termites to rebuild some parts of their nest and allowed time to assess agonism between colonies in laboratory bioassays conducted as described above. After the acclimatization period, a stick was positioned to connect each nest with the ground so that they were 80 cm apart. Some individuals from each colonies were marked with yellow and red Magix® color spray. We tested the outcome of encounters between foragers of nests which appeared to be anagonists, moderate agonists and strong agonists in laboratory bioassays. We focused on *N. princeps* (10 nests paired) because this species is more common in plantations than *N. novarumhebridarum* (2 anagonist nests paired).

Small trees supporting *M. biroi* nests were cut in a secondary forest and brought to Laing Island. The volume of collected nests ranged between 13 and 35 liters. On Laing Island, nests were hung with a rope to a portico (Fig. 25d). Eight baits composed of small pieces of wood were arranged along a circle (radius: 70 cm) at the center of the set-up. A barrier of water around the rope prevented escapes of termites and attacks by ants during a 2 day acclimatization period during which laboratory bioassays were conducted. Sticks were then installed to connect the nests to the ground. Sticks at a distance of 15 cm in two initial tests were placed 50 cm apart in the following tests because 15 cm did not provide enough opportunity for termites from the two nests to avoid each other. We did not succeed in finding anagonist *M. biroi* nests in the forest for these experiments.

Results

Agonism between *N. princeps* colonies

Aggressive behaviors

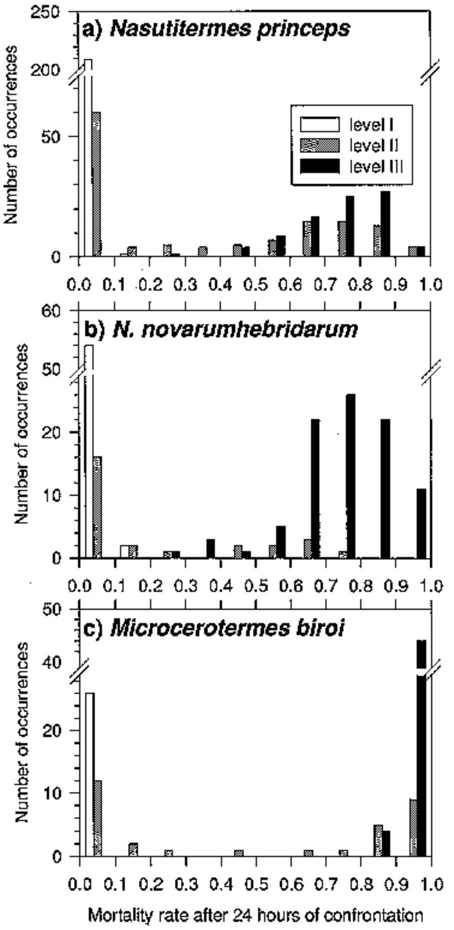

Figure 26: Histogram of mortality rate due to anagonism (level I), moderate agonism (level II) and strong agonism (level III) after 24 hours confrontations in laboratory bioassay for: a) *N. princeps*; b) *N. novarumhebridarum*; c) *M. biroi* colonies.

In anagonistic encounters (level I), groups of termites from two different nests behaved as in controls: during the first encounters, they showed some excitement by displaying oscillatory movements that dissipated rapidly as the two groups mixed together. Death rates of groups of soldiers and workers in anagonistic encounters was 0.02 ± 0.02 (average ± standard deviation) (n= 210) (Fig. 26a), which were not significantly different from controls 0.02 ± 0.02 (n= 160) (t-value= 0.81, df= 368, P= 0.421). In moderately agonistic encounters (level II), some *N. princeps* individuals reacted to the presence of aliens while others did not. Discriminatory behaviors never arose without contact with an alien. Aliens were sometimes examined for a prolonged period (for more than 10 seconds). After discrimination, three levels of increasing aggressiveness could be reached: (i) nipping or avoidance, (ii) alarm: termites jerked back when they touched an alien and displayed an increased walking speed or a faster oscillatory movement, (iii) attack, i.e. bites by workers, causing severe wounds, or projection of defensive secretion by nasute soldiers. A wide range of aggressive responses was observed in bioassays with moderately agonistic colonies: in some cases, a few termites were very aggressive and the others apparently indifferent, in other cases, most of the termites displayed mild agonistic behavior. Video recordings showed that aggressiveness was sometimes high but delayed for up to 10 minutes after initial contact. Death rate in moderately agonistic encounters was variable (0.36 ± 0.34, n= 132) and bimodally distributed (Fig. 26a): in some bioassays, individuals showing initial aggressiveness either calmed down or were killed in fights without eliciting further aggression, and mortality was low; in other tests, alarm and aggression, though initially low or restricted to a few individuals, propagated until generalized fighting erupted, and resulting mortality was high. Very variable responses were sometimes observed among replicates involving the same colonies; as an example, between moderately agonistic nests laboratory bioassays revealed the following results: nest V vs. nest VI: 4 replicates with neither initial aggressiveness nor high final mortality, 2 replicates with initial aggressiveness but no mortality, 8 replicates with initial aggressiveness and high final mortality, 1 replicate without initial aggressiveness but high final mortality due to fighting; for nests VII and VIII the number of replicates falling in each category was respectively: 5, 4, 6, 0. In strongly agonistic encounters, a large number of *N. princeps* were aggressive after a short period of contact with aliens and resulting mortality was invariably high (0.74 ± 0.13, n=87) (Fig. 26a).

Frequency of agonism in laboratory bioassays

N. princeps colonies coming from 4 sites were confronted in laboratory bioassays during two consecutive seasons (Fig.27). Site A2 was unique for its abundance of *N. princeps*: 112 nests were recorded on 3.1 ha in 1991. The map presented in fig. 27 shows a portion of this site where 86 nests were present. No agonism was detected in any of the 40 combinations tested between the 15 largest nests (Fig. 27). Ten of these nests were opened and all were polygynous, containing large numbers of adultoid reproductives. At the three other sites, agonism (level II or III) was observed for 41 of 52 (79%) combinations tested. Moderate agonism occurred in 17 combinations, especially at site P1 where 9 of 10 confrontations were moderately agonistic. Lack of agonism was observed in 1 of 16 combinations between neighboring colonies (Fig. 27) and in 10 of 36 combinations (not represented on Fig. 27 for reason of clarity) between geographically distant colonies. These proportions are not significantly different (Fisher's exact test, P= 0.140).

Agonistic reactions were consistent during the two consecutive seasons: 48 of 50 combinations tested in July-August 1991 yielded the same results in February-March 1992. In the two remaining combinations, between distant colonies coming from sites A2 and B4, agonism decreased (level III in 1991 to level II in 1992) or vanished (level II in 1991 to level I in 1992).

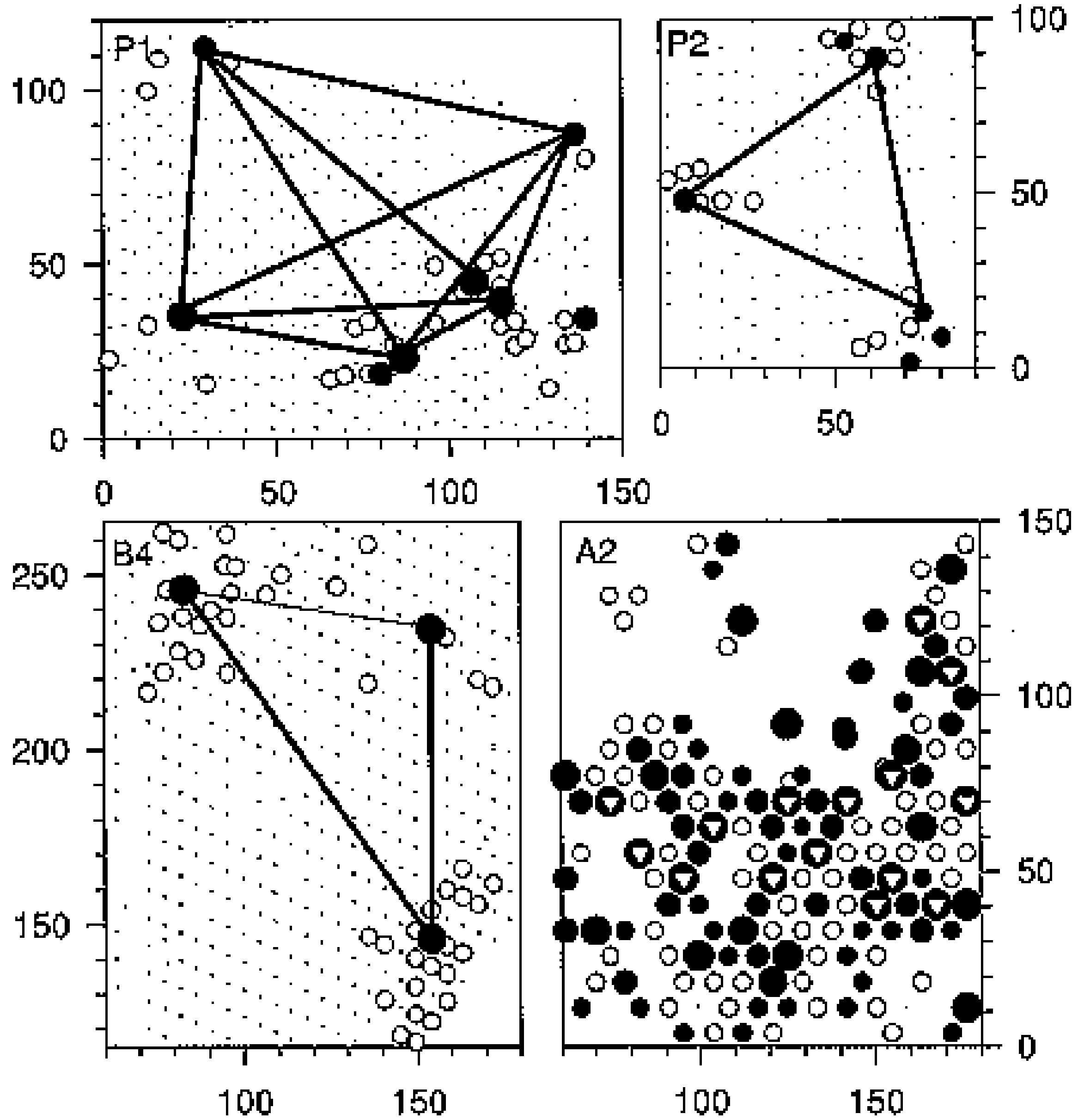

Figure 27: Agonism between neighbor *N. princeps* colonies at 4 sites: P1, P2, B4 and A2. Symbols: closed circle: tree supporting a *N. princeps* nest; open circle: tree covered with *N. princeps* galleries; dot: tree not occupied by *N. princeps*. A thin line between two nests indicates absence of agonism (level I), a thick line indicates agonism (level II or III). At site A2, 40 combinations between nests marked with a triangle yielded no agonism; for clarity corresponding thin lines were not drawn on the map.

Agonistic reactions between entire nest populations

Exploratory trails from *N. princeps* nests that were anagonistic in laboratory bioassays (I vs. II, III vs. IV, table 9) immediately huddled without aggressiveness when they encountered on the 9 m^2 experimental area. Foragers included workers, soldiers, nymphs and, in the assay involving nests I and II, even alates. During the 9 days that these two confrontations lasted, exchanges of marked individuals between the nests were frequent, although this was sometimes interrupted by sunlight on termite foraging trails (which were not covered).

The outcome of encounters between two pairs of nests that were moderately agonistic in laboratory bioassays differed in the field (V vs. VI and VII vs. VIII, table 9). The first encounters between foragers coming from both paired nests resulted in many fights. However, in confrontations involving nests V and VI, the allocolonial termites mixed 3 hours later, whereas in confrontation involving nests VII and VIII, allocolonial trails met again on several occasions but termites always fought and trails diverged afterwards (Fig. 28). Colonies V and VI remained in contact during the 13 days duration of the experiment, apparently because the number of aggressive indivi-duals gradually decreased (presumably because they calmed down or were eliminated).

Individuals from two nests that were strongly agonistic in laboratory tests (IX vs. X, table 9) also fought in semi-natural conditions: battle-fields of up to 35 cm radius, covered with corpses, were observed on several occa-sions and trails always diverged afterwards.

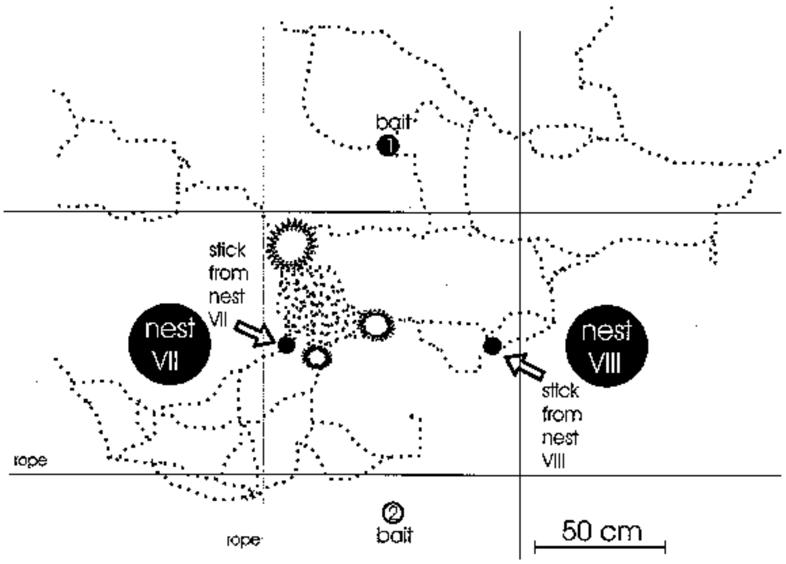

Figure 28: Confrontation in semi-natural conditions of *N. princeps* nests VII and VIII, moderately agonists in laboratory bioassays. Aerial view of non-covered gallery network (dotted lines) departing from each nest 7½ hours after the experiment initiation. Stars indicate places where allocolonial fighting occured.

All confronted nests were originally headed by reproductives; however, they died during the course of the experiment in 3 nests (table 9), either because the royal cell was damaged during the collection of the nest or because nests finally desiccated.

Table 9: Comparison of tests with groups of individuals in the laboratory versus entire nest population on a 9m^2 experimental area.

nests			laboratory	9m^2 experimental area		reproductive status*	
A	vs	B	agonism	first encounters	outcome after 24 hours	nest A	nest B
N. princeps							
I	vs.	II	absent	huddling	exchange of neuters, nymphs and alates	polygynous	polygynous
III	vs.	IV	absent	huddling	exchange of neuters and nymphs	polygynous	polygynous
V	vs.	VI	moderate	fighting	exchange of neuters and nymphs	polygynous	? **
VII	vs.	VIII	moderate	fighting	exclusion: trail divergence	? ***	? ***
IX	vs.	X	strong	fighting	exclusion: trail divergence	polygynous	polygynous
N. novarumhebridarum							
XI	vs.	XII	absent	huddling	exchange of neuters and nymphs	monogynous	monogynous
M. biroi							
XIII	vs.	XIV	not tested	fighting	nest attack	queen(s) killed ?	polygynous
XV	vs.	XVI	strong	fighting	nest attack	monogynous	queen(s) killed ?
XVII	vs.	XVIII	strong	fighting	exclusion: trail divergence	?	?

* nests dissected at the end of the experimental period (4 days - 3 weeks), **: royal cell damaged during collection, ***: nests died of desiccation

Agonism between *N. novarumhebridarum* colonies

Aggressive behaviors

Individual aggressive behaviors in *N. novarumhebridarum* were similar to those observed in *N. princeps*. Death rates for anagonistic encounters (level I) were 0.03 ± 0.04 (n= 56) (Fig. 26b), which were not significantly different from controls 0.04 ± 0.04 (n= 54) (t = 0.86, df= 108, P= 0.390). Death rates were variable in moderately agonistic (level II) encounters (0.22 ± 0.27 n= 27) and high (0.76 ± 0.14 n = 91) in strongly agonistic ones (level III) (Fig. 26b).

Frequency of agonism in laboratory bioassays

Fourty-one pairings between *N. novarumhebridarum* nests were performed in 1991, 25 of which were repeated the next season. Lack of agonism was observed in 6 of 21 combinations between strangers and in 8 of 20 combinations between neighbors (Fig.29). These proportions are not significantly different (Pearson's Chi Square = 0.595, P = 0.440). Overall, agonism occurred in 27 of 41 (66%) combinations tested, comprising 4 cases of moderate agonism and 23 cases of strong agonism. Agonistic reactions were consistent in time: 24 of 25 combinations tested in June-July 1991 yielded the same results in March-April 1992. In one case, moderate instead of strong agonism was observed. Furthermore, nests XI and XII which were anagonists in 1991 were confronted 3 years later and were still mutually tolerant.

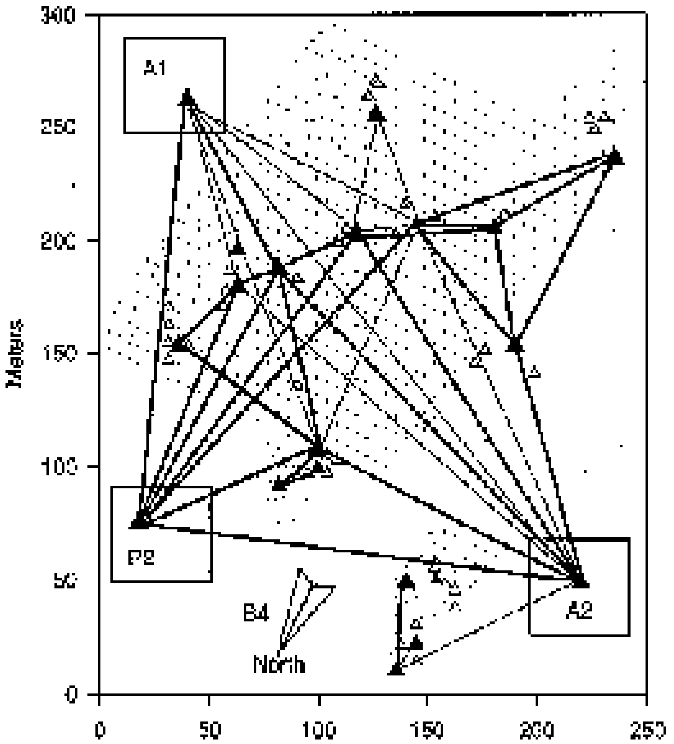

Figure 29: Agonism between neighbor *N. novarumhebridarum* colonies at site B4 and between these colonies and stranger colonies from sites A1, A2 and P2. Symbols: closed triangle: tree supporting a *N. novarumhebridarum* nest; open triangle: tree covered with *N. novarumhebridarum* galleries; dot: tree not occupied by *N. novarum-hebridarum*. A thin line between two nests indicates absence of agonism (level I), a thick line indicates agonism (level II or III).

Agonistic reactions between entire nest populations

Foragers from both nests XI and XII (table 9), anagonists in laboratory, met without any manifestation of aggressiveness on the 9 m² experimental area. The two nests remained connected during the four days duration of the experiment. The foraging trails were found partly covered 12 hours after the first encounters and building activity continued afterwards, although it sometimes was interrupted during the day because of direct sunlight exposure and predation by lizards.

Agonism between *M. biroi* colonies

Aggressive behaviors

By contrast with the two *Nasutitermes* species, *M. biroi* soldiers are proportionally less numerous and use their large mandibles as mechanical weapons rather than squirting a defensive secretion. In anagonistic encounters (level I), termites behaved as in controls: they were apparently mutually tolerant and showed some excitement (forward and backward body oscillation) when initially meeting the other group; this excitement disappeared as the two groups huddled. Allocolonial grooming (e.g. licking) was sometimes noticed during these anagonistic encounters. Death rates in anagonistic encounters were 0.01± 0.02 (n= 26) (Fig.26c), which were not significantly different from controls (0.02 ± 0.02, n= 32) (t= 1.11, df= 56, P= 0.272). In moderately agonistic encounters (level II), the death rates were strongly bimodal (0.50 ± 0.43, n= 32) (Fig.26c). In some tests, only a few pairs fought among the mixed group. Because bites from workers or soldiers were often fatal, the few aggressive individuals usually died leaving only tolerant individuals behind, which resulted in low mortality. In other tests, aggressiveness appeared very gradually: individuals were apparently tolerant during the first encounters, but started to nip or even to bite severely after 10 to 60 minutes of contact, resulting in a generalized battle with high mortality. As in the two *Nasutitermes* species, replicates between moderately agonistic *M. biroi* colonies sometimes yielded very variable, apparently contradictory, results. In strongly agonistic encounters, general aggressiveness rose rapidly, resulting in a high death rate (0.96 ± 0.03, n=48) (Fig.26c). In two very agonistic encounters, 1 to 2 of the 12 soldiers present were observed banging their head on the substratum.

Frequency of agonism in laboratory bioassays

Lack of agonism was observed in 1 of 14 combinations between non-neighbors (from sites N1 and P3) and in 8 of 21 combinations between neighbors at site N2 (Fisher's exact test, P= 0.056) (Fig. 30). Altogether, 26 of 35 (74%) combinations were agonistic. Moderate agonism was observed in 9 of these agonistic combinations.

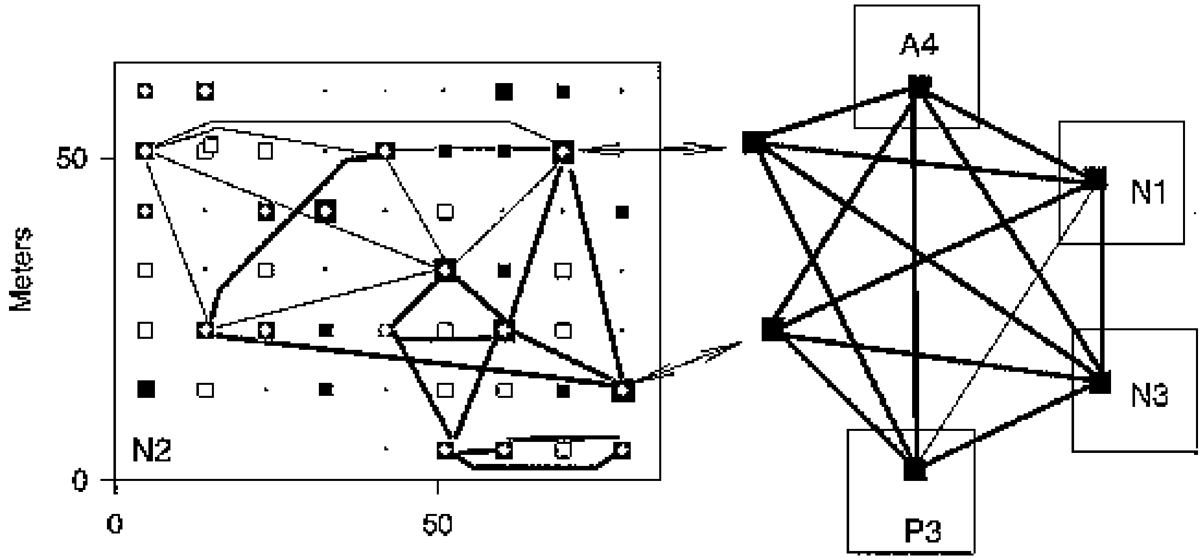

Figure 30: Agonism between neighbor *M. biroi* colonies in site N2 and between two of these colonies and stranger colonies from sites A4, N1, N3 and P3. Symbols: closed square: tree supporting a *M. biroi* nest; diamond: nest with reproductives; open square: tree covered with *M. biroi* galleries; dot: tree not occupied by *M. biroi*. A thin line between two nests indicates absence of agonism (level I), a thick line indicates agonism (level II or III).

Agonistic reactions between entire nest populations

Three pairs of *M. biroi* nests were confronted in semi-natural conditions: two pairs exhibited strong agonism in laboratory bioassays (nests XV vs. XVI and XVII vs. XVIII, table 9), the other pair (nests XIII vs. XIV, table 9) which were not tested in laboratory, diplayed aggressiveness in semi-natural conditions.

When sticks departing from each nest were separated by only 15cm at the ground level, confronted colonies (XIII vs. XIV and XV vs. XVI) tried to destroy each other. In both confrontations, a few hours after the first encounters, members from one nest built covered galleries in the direction of the stick leading to the other nest, which then was attacked. Fierce battles proceeded during the remainder of the experimental period. Thirteen days after the beginning of the confrontation, all 4 nests were dissected and found to contain live termites and egg masses. Both nests XIII and XIV contained corpses of fighters. Individuals from these two nests fought when combined in a Petri dish arena. Only nest XIV was still headed by a queen. By contrast, individuals from nests XV and XVI did not fight anymore in laboratory bioassays. Nest XV still contained a queen and was devoid of corpses, but nest XVI lost its queen and contained many dead bodies.

When sticks departing from each nest were separated by 50 cm at the ground level (nests XVII vs. XVIII, table 9), no nest attack was observed. At the beginning of the confrontations, trails from the two nests met at several points, resulting in fighting (Fig. 31a) and leading to a rearrangement of each colony gallery network (Fig. 31b), which finally stabilized and diverged (Fig. 31c). During intense fights between allocolonial termites in the three pairings, the clicking sound of soldiers head-banging was heard in the nests.

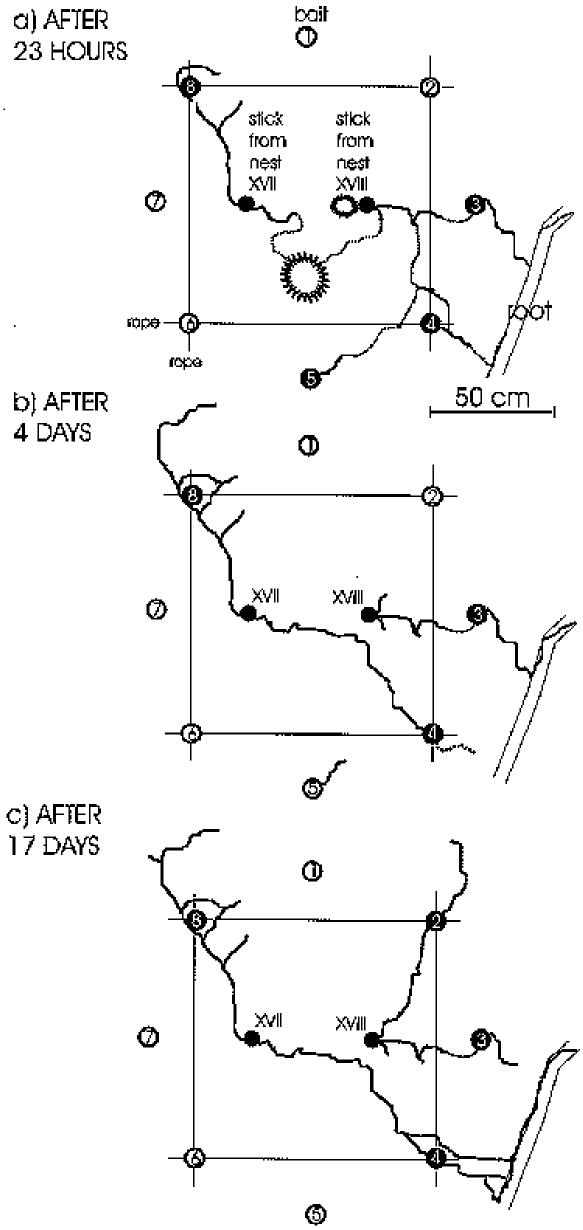

Figure 31: Confrontation in semi-natural conditions of *M. biroi* nests XVII and XVIII, agonists in laboratory bioassays. Aerial view of covered (solid line) and non-covered (dotted line) gallery network departing from each nest 23 hours (a), 4 days (b) and 17 days (c) after the beginning of the experiment. The location of intercolonial fights is indicated with stars.

Discussion

Aggressive behavior

Results of laboratory bioassays were consistent with the outcome of allocolonial encounters in semi-natural conditions: anagonistic *N. princeps* or *N. novarumhebridarum* groups joined, whereas strongly agonistic *N. princeps* or *M. biroi* groups avoided or tended to destroy each other. Moderately agonistic *N. princeps* colonies either joined after fighting or avoided each other.

Agonistic reactions between conspecific colonies of three arboreal-nesting termitids were variable, ranging from anagonism to strong agonism. Such variability has also been reported in other Termitidae (Andrews 1911; Nel 1968; Thorne 1982a), in Rhinotermitidae (Su & Scheffrahn 1988, Su & Haverty 1991), in Termopsidae (Haverty & Thorne 1989), and in Hodotermitidae (Nel 1968). Whereas it was easy to define the lowest and highest grades of agonism (respectively, level I and level III), pairwise encounters also yielded a wide range of intermediate responses, which we called moderate agonism (level II). Su & Haverty (1991) also observed that in encounters between allocolonial *Coptotermes formosanus*, initially aggressive pairings could result in low mortality, or conversely, some initially passive encounters could result in mortality due to fighting. These authors proposed that a stimulus eliciting initial aggression, received upon contact with an alien, must be reinforced by another stimulus for aggression to continue. The fact that the distribution of mortality rates was clearly bimodal, at least in *N. princeps* and *M. biroi*, pinpoints the existence of collective mechanisms leading either to the extinction of aggressive behaviors (as the most aggressive individuals calm down or are killed) or to their amplification until generalized fighting erupts. Such mechanisms of collective decision are widespread in social insects, where their importance is best known in foraging and construction behavior; one of their general properties is high sensitivity to past events (often random ones) and environmental conditions (Deneubourg & Goss 1989). In the present case, the collective decision (i.e., whether alarm and aggressiveness will rise to generalized fighting or not) may depend on a large number of factors. Average aggressiveness or discriminatory ability may vary among colonies due to differences in genetic composition, age, health, nutrition, reproductive status, or environmental influences (Thorne 1982a; Thorne & Haverty 1991); individuals may vary within a colony for the same reasons; and even if were possible to trigger confrontations repeatedly under similar conditions between the same groups of individuals, their outcome could vary by chance, depending on which individuals encountered each other and when. The fact that each colony is somehow heterogenous itself (especially in polygynous and polydomous species, such as *N. princeps*) might explain why tolerance or rejection of members of another group is a matter of collective decision.

The participation of both soldiers and workers in colony defense is a common feature of termites (Andrews 1911, Eisner *et al.* 1976, Thorne 1982a, Traniello & Beshers 1985). *Nasutitermes* soldiers squirt a sticky defensive secretion on their enemies. The chemical composition of this secretion is colony-specific (Pasteels *et al.* 1988, Everaerts *et al.* 1988a, Roisin *et al.* 1990), but it is not known if termites use it as a complementary cue to detect the presence of aliens. It has previously been shown that the frontal gland secretion acts as a pheromone in *N. princeps*, alarming and recruiting workers (Roisin *et al.* 1990), but this secretion has no such pheromonal action in *N. novarumhebridarum* (annexe **7**). *M. biroi* soldiers were observed banging their head against the substrate. This behavior was also noticed during interspecific encounters with *N. princeps* (chapter **2**). Although exceptional in laboratory bioassays, head banging was observed during all three confrontations between entire nests of *M. biroi* when one of the nests was under attack. However, under these circumstances, it could have been triggered either by encounters with conspecifics, by encounters with predatory ants, or by mechanical disturbance caused by nest transportation.

Influence of intraspecific agonism on community structure

All three species showed comparable levels of intraspecific agonism: 79% of the combinations tested in *N. princeps*, 66% in *N. novarumhebridarum*, and 74% in *M. biroi* were agonistic. Agonism in *N. princeps* and *N. novarumhebridarum* did not vary seasonally and in all three species, distant nests, unlikely to be genetically closely related, were not more often agonistic than nests from the same site. Intraspecific agonism should complement interspecific exclusion in shaping colony distribution in this community of arboreal termites.

Because of the high density of *M. biroi* colonies in plantations, encounters between foraging parties are very likely. For encounters between agonistic colonies, one of our experiments in semi-natural conditions indicates that trails will probably diverge after fights. Nevertheless, when nests are too close, they apparently tend to eliminate each other: the colony from nest XIII attempted to invade nest XIV, whereas individuals from nest XV were apparently able to take over nest XVI (table 9). In the field, the fact that any single tree never supports more than one *M. biroi* colony (chapter **4**) constitutes evidence for competitive exclusion. However, the frequency of nest invasion remains uncertain. Neither actual fights between colonies of *M. biroi* nor signs of recent battles were ever witnessed in the field, in spite of the careful inspection of more than 2000 nests of this species. Some trees were found supporting two nests, one of which was headed by a royal pair while the other contained an empty royal cell (chapter **4**): such findings may indicate that one colony killed the other, but it also may indicate colonization of a previously abandoned nest. A likely hypothesis is that competitive exclusion most frequently eliminates young colonies before they have built an apparent nest, but seldom leads to the death of a mature colony.

No naturally occurring fights were observed between mature colonies of *Nasutitermes* either. The scarcity of intercolonial fighting in *N. novarumhebridarum* can be explained by the relative sparseness of this species, which preferentially colonizes dead trees (chapter **3**). Fights are probably more likely to occur between neighboring colonies of *N. princeps*, especially as those colonies attempt to expand their territory by constructing additional nests leading to polydomous colonies. However, such fights may be mostly limited to foraging trails and thus have little chance to proceed to nest elimination, except for the weakest (youngest, smallest) colonies. High densities of *N. princeps* nests such as in site A2 are probably possible only if nests are mutually anagonists, forming a supercolony. Supercolonies might also exist in other highly polygynous termite species such as *N. corniger*, *N. costalis* and in *N. polygynus* where high nest concentrations have also been observed (Thorne 1982b, Roisin & Pasteels 1986b).

Trail divergence, consistent with other authors' data on Neotropical species (Thorne 1982a, Levings & Adams 1984), is probably a mechanism to minimize warfare and allow each colony to maintain its own definite territory. The resulting pattern of territories observed in Neo-Guinean arboreal nesting termites (chapter **2**) recalls mosaics described in other termite communities (Levings & Adams 1984, Jones 1990, 1993, Jones & Trosset 1991) and tropical ants (Majer 1993, Adams 1994a).

Besides nest elimination or trail divergence, our experiments suggested that intercolonial encounters may have the outcome of colony fusion. This possibility was pinpointed by our experiments with *N. princeps* and *N. novarumhebridarum*. This phenomenon was actually observed by Su & Scheffrahn (1988) in *Coptotermes formosanus* in Florida. However, in that case, the involved colonies were part of a population most likely derived from a single recent introduction, and thus highly related. Our experiments suggest that distant colonies of

N. princeps, unlikely to be related, are sometimes anagonistic and are able to merge and to exchange alates. Considering the ability of *N. princeps* to produce two alate morphs (short- and long-winged) which readily assume reproduction in queenless nests (Roisin & Pasteels 1985a, 1986a), the possibility exists that transfer of alates may occur between neighboring colonies, leading to outbreeding without nuptial flights when alates become secondary reproductives during budding or replacement of reproductives. Genetic studies would be best suited to investigate this hypothesis, which casts doubt on the generally accepted rule that termite colonies are tightly closed to foreign genes (Roisin 1993).

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6. Interference of ants with arboreal-nesting termites in New Guinean coconut plantations.

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M. Leponce, Y. Roisin, and J. M. Pasteels

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Introduction

Ants are known as major termite predators (Wheeler 1936, Wood & Sands 1978, Deligne *et al.* 1981, Nutting & Jones 1990) and are sometimes reported as the principal cause of termite nest mortality (Darlington 1985b). After studying the effect of the environment (chapter 3), of inter- and intra-specific competition (chapters 2 and 5), we intended to evaluate the interference of ants with an arboreal-nesting termite community living in New Guinea coconut plantations. The termite community is composed of three species: *Microcerotermes biroi* (Desneux), *Nasutitermes princeps* (Desneux) and *N. novarumhebridarum* (N. & K. Holmgren). All build carton nests from which depart covered galleries. These galleries either reach the top of the trees or the ground where they often lead to adjacent trees. The abundance of termite colonies is affected by habitat structure: in open plantations (density ≤ 100 trees/ha), on average 25% of the trees are occupied by arboreal termites, whereas in denser habitats (>100 trees/ha), 56% of the trees are occupied (chapter 3). Interspecific competition leads to the destruction of *M. biroi* colonies by neighbour *Nasutitermes* colonies (chapter 2) whereas intraspecific competition results in trail divergence and probably in the elimination of the weakest colonies (chapter 5). Besides termite colonies, coconut plantations may also harbour numerous ant species: for example, 65 species were recorded in such plantations in the Solomon Islands (Brown 1959a). Several ant species, e.g. *Oecophylla smaragdina* (F.), are omnipresent in coconut plantations on the north coast of New Guinea but are only occasional termite predators because termites stay under the shelter of their galleries rather than forage in the open. However two categories of ants are likely to interact strongly with termites: inquiline ants, which inhabit termite nests, and arboreal-nesting ants, which build their nest on the same tree as termites. We first assessed the frequency of inquiline ants in termite nests and monitored nests containing the commonest inquiline ant to define the outcome of the cohabitation between termites and ants. Second, we compared termite abundance in sites invaded by or devoid of the most abundant arboreal nesting ant species and studied the dynamics of the cohabitation between ants and termites.

Results and discussion

The observations were conducted in coconut plantations along the north coast of New Guinea near Hansa Bay, Bogia district, Madang Province.

Inquiline ants

The presence of inquiline ants was systematically checked in all *M. biroi* and *N. princeps* nests present in 8 sites of 1 ha randomly selected and in 1 site of 3 ha chosen for the abundance of *N. princeps* nests. Ants were detected by making superficial cuts (2 - 3 cm deep) all over the nest surface. Ants coming out of the nest were collected and preserved in 70% ethanol for later identification. Voucher specimens were deposited in our laboratory. Small populations of tiny ants, which did not seem to exert much influence on termite population, were disregarded from this sampling. Inquiline ants were found in 44 of 462 (9.6%) *M. biroi* nests sampled and in 6 of 120 (5.0%) *N. princeps* nests sampled. Two factors might explain why inquilines are found two times more often in nests of *M. biroi* than in nests of *N. princeps*. First, the defensive secretion of *Nasutitermes* soldiers has proved to be an effective weapon against ants (Eisner *et al.* 1976, Mill 1983, Everaerts *et al.* 1988b, 1990, Valterová *et al.* 1989, Jaffe *et al.* 1995) especially in species such as *N. princeps* where its pheromonal role allow a coordinated warfare between soldiers and workers (Roisin *et al.* 1990). Second, it might be more difficult for the ants to isolate themselves from the termite colony in *N. princeps* nests where the communication openings between chambers are much wider than in *M. biroi* nests (Deligne & Pasteels 1982). Carpenter ants were the commonest inquilines: *Camponotus* sp. A was found in 23 *M. biroi* nests and in 5 *N. princeps* nests; *Camponotus* sp. B was found in 9 *M. biroi* nests. *Philidris* (formerly *Iridomyrmex*) *cordatus* (Smith) was found in 4 *M. biroi* nests and in 1 *N. princeps* nest. Other species found in

M. biroi nests included *Calomyrmex* sp., *Papyrius nitidus* and *Tapinoma* sp.. The presence of *Camponotus* sp. A could often be detected by the presence of a different building material than the termite carton on breaches in the nest envelope. Coccids were also present on the tree trunk inside termite nests and galleries invaded with *Camponotus* sp. A. This ant was sometimes found outside termite nests in rotten wood under the tree bark. Single queens of *Camponotus* sp. A were sometimes found in *M. biroi* nests.

Nests of *M. biroi* and *N. princeps* found with *Camponotus* sp. A were monitored for up to 3 years. *N. novarumhebridarum* nests were not sampled because of their low abundance in plantations (chapter 3). To minimize the effects of the disturbance caused by sampling, the nests were only checked after long intervals of 6 to 30 months. *Camponotus* sp. A was observed coexisting for 6 months to 19 months (*M. biroi*) or 35 months (*N. princeps*) with its host (Table 10) and therefore does not appear as an immediate threat to the termite population. Furthermore, *Camponotus* sp. A either left or was expelled from the termite nest after a few months in, respectively, 45% and 75% of the 22 *M. biroi* and 12 *N. princeps* monitored. However, 6 of the *M. biroi* nests which contained *Camponotus* sp. A collapsed; 3 of these nests were still on the tree and contained the inquiline ants 13 to 24 months later, while the other 3 fell to the ground and were found empty. The possibility of destruction of the termite populations by *Camponotus* sp. A in these nests should not be rejected. The death of 3 other *M. biroi* nests was caused by *N. princeps* while one of the *N. princeps* nests monitored died for unknown reasons.

Table 10: Coexistence of *Camponotus* sp. A ants and termites in 22 *M. biroi* nests and in 12 *N. princeps* nests monitored for up to 3 years.

Outcome of nests occupied by ants and termites	*M. biroi* nests	*N. princeps* nests
status quo *	3	2
abandoned only by ants	10	9
abandoned only by termites	3	0
dead	3	1
colonized by the other termite species	3	0
Total number of nests	22	12

* Nests reported as status quo were followed for at least 19 months (*M. biroi*) or 35 months (*N. princeps*).

Camponotus sp. A is not an obligatory inquiline. Opportunistic inquilinism was also reported for inquiline ants of *Nasutitermes corniger* in Brazil which inhabited a higher proportion of nests in flooded areas and during the wet season (Jaffe *et al.* 1995). Although it has long been thought that inquilinism was only beneficial for the ant, finding shelter and food in the termitaria, recent studies have shown that inquiline ants might have a beneficial incidence on their host by protecting it against raids of other ant species or by bringing nitrogen-rich food (ant corpses and middens) into the nest (Higashi & Ito 1989, Jaffe *et al.* 1995). Such a mutualistic relationship was not investigated here.

Arboreal-nesting ants

Coconut plantations around Hansa Bay were also scanned for the presence of arboreal-nesting ants. Three arboreal-nesting *Crematogaster* species (sp. A, B, C) and *Papyrius* (formerly *Iridomyrmex*) *nitidus* (Mayr) were observed. Only *Crematogaster* sp. A was found occupying large areas of coconut plantations. Spots heavily colonized by *Crematogaster* sp. A in coconut plantations were uncommon. This habitat is probably marginal for these ants which seemed more abundant on cocoa. A high population density of these ants was only observed in coconut plantations adjoining a cocoa plantation. *Crematogaster* sp. A built its nests on the trunk and on the palm leaves at the top of the tree. *Crematogaster* sp. A preyed on termites whose nest or galleries were artificially opened. On some occasions it was observed building its carton nest on a live termite nest which was then progressively invaded. In order to evaluate the possible impact of *Crematogaster* sp. A on the termite community, we selected 2 sites heavily invaded by this ant: site Bogia 1 in an open plantation (0.8 ha, 96 trees/ha, tall trees >20 m in height) and site Bogia 6 in a dense plantation (1.0 ha, 202 trees/ha, trees 13-25 m in height). Ant and termite nests and trails were mapped in September 1990, April 1993 and April 1994 in site Bogia 1 and in April 1993 and April 1994 in site Bogia 6. Observations were performed during day time by sunny weather to compare the ant activity in similar conditions. In site Bogia 1 (Fig. 32), in September 1990, *Crematogaster* sp. A occupied 77 % of the trees present whereas arboreal-nesting termites occupied 11% of them. Thirty-one months later, in April 1993, 96% of the trees were occupied by ants and 9% by termites. None of the 1990's *M. biroi* colonies survived but three nests, one of each termite species, developed in the meantime. In 1994, fewer trees, 83%, were occupied by *Crematogaster* sp. A and a few more, 15%, by termites. In site Bogia 6 (Fig. 33) *Crematogaster* sp. A nests or trails were found on 99% of the trees in 1993 and on 96% in 1994; however the number of trees supporting ant nests increased from 146 to 161. During the same time lapse trees occupied by termites decreased from 27% to 21%. The disappearance/appearance of a termite nest between 1993 and 1994 was significantly related with the presence/absence of an ant nest on a tree in 1994 (Fisher's exact test P=0.02). In Bogia 1, such a relationship could not be investigated due to the small sample size. However, in both sites Bogia 1 and Bogia 6, the absence/presence of termite nest at a particular time was independent of the presence/absence of ant nests (Fisher's exact tests, P > 0.05) probably because ants should have no difficulty to establish on a tree occupied by termites.

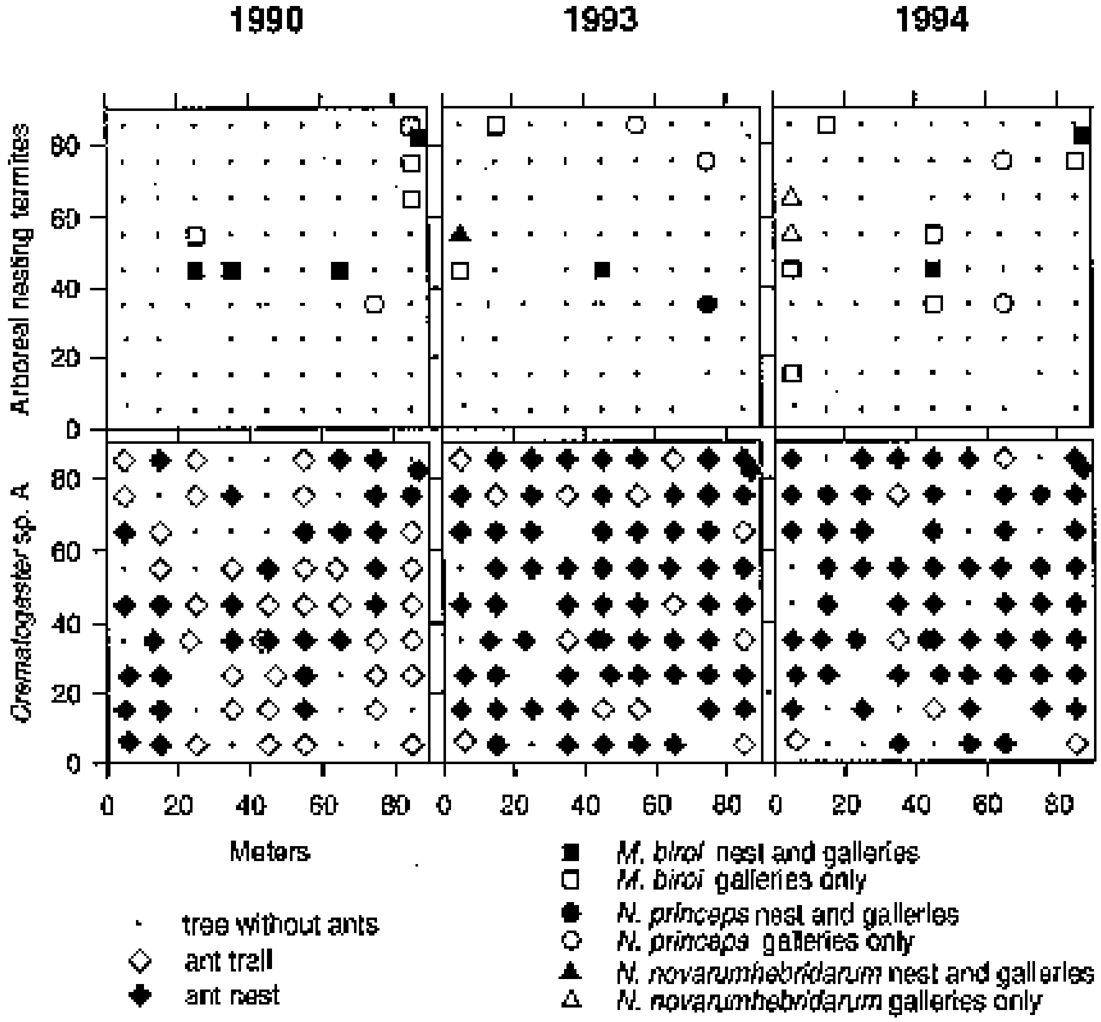

Figure 32: Map of occupation of site Bogia 1 by arboreal nesting termites and *Crematogaster sp.A* in September 1990, April 1993 and April 1994. Maps of termite (at top) and ant (at bottom) colonies were separated for clarity.

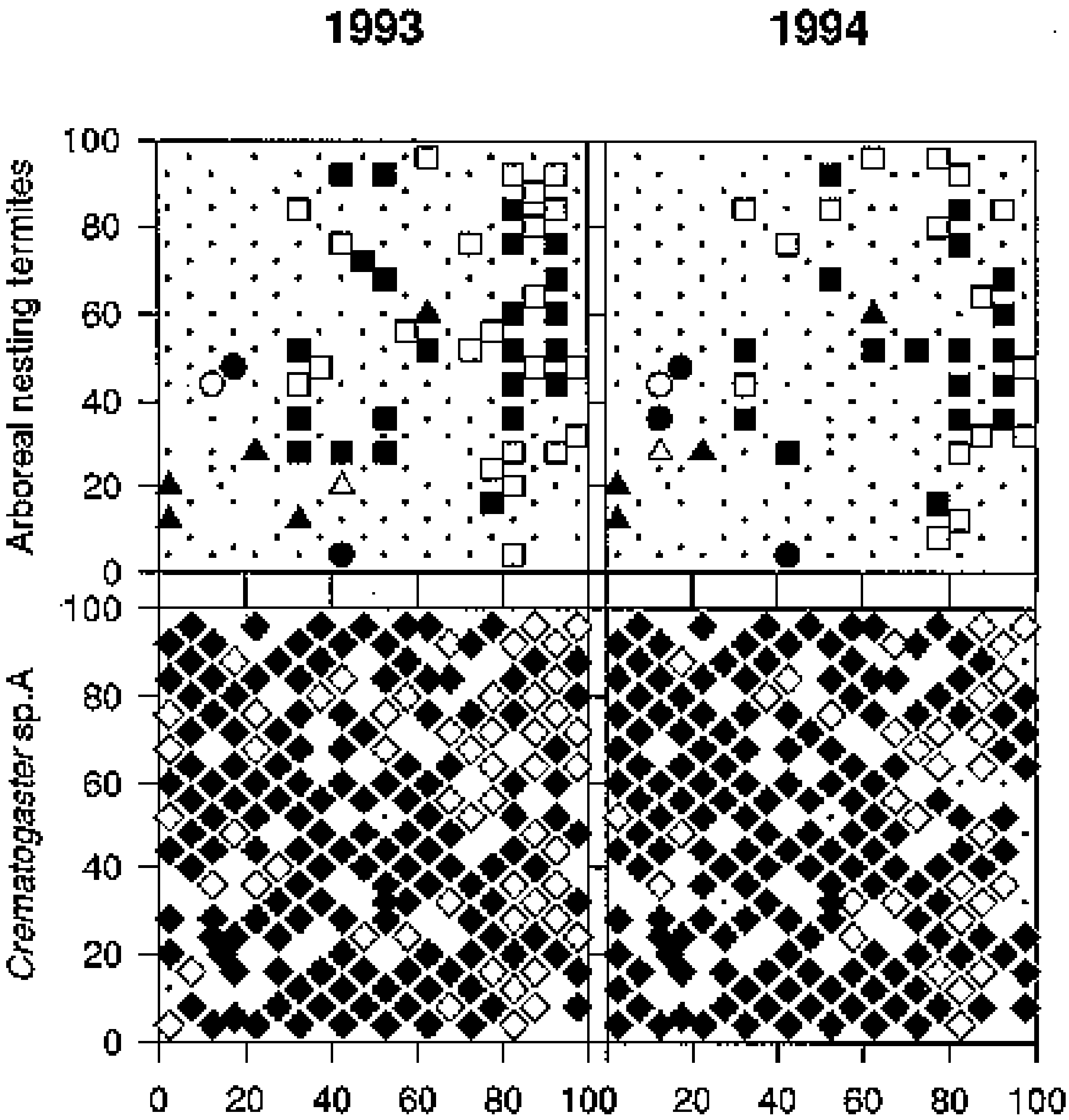

Figure 33: Map of occupation of site Bogia 6 by arboreal nesting termites and *Crematogaster sp.A* in April 1993 and April 1994. Legend as in Fig. 32.

Termite abundance in Bogia 1 and Bogia 6 was compared to termite abundance in, respectively, 5 open and 5 dense plots of 1 ha (for more details about these 10 plots, see chapter 3), devoid of arboreal ants but very similar in other respects. In sites invaded by *Crematogaster* sp. A the proportion of trees occupied by arboreal termites was half lower: on average 11.8 % in Bogia 1 versus 24.9% in open plantations without *Crematogaster* sp. A and 23.5 % in Bogia 6 versus 53.6 % in dense plantations without *Crematogaster* sp. A. Other environmental factors than the presence of ants apparently did not interfere severely with termite populations during the observation period, which suggests that the presence of *Crematogaster* sp. A markedly affected the overall abundance of termites in Bogia 1 and Bogia 6. The presence of *Crematogaster* sp. A apparently did not affect the ratio between

M. biroi : *N. princeps* : *N. novarumhebridarum*. This ratio was 66: 24: 10 (average, n= 3, replicates of 1990, 1993 and 1994) in Bogia 1 and 81 : 7 : 11 in Bogia 6 (n= 2, replicates of 1993 and 1994). These ratios are not significantly different from respectively open and dense plantations without *Crematogaster* sp. A (see chapter 3) (t-tests P> 0.05). The fact that the ratio between the three termite species was unaffected by the presence or absence of *Crematogaster* sp. A suggests a similar resistance of the 3 species towards the ant.

These results suggest that the defensive mechanisms of *N. princeps*, although more effective than those of *M. biroi* to keep away inquiline ants, might not be sufficient to prevent a high population density of *Crematogaster* sp. A from limiting its abundance in coconut plantations. Although the impact of ants on the arboreal-nesting termite community was generally mild compared to environmental influences (chapter 3) and termite-termite interactions (chapters 2 and 5), *Crematogaster* sp. A may substantially lower the termite population in some habitats.

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7. Discussion générale

Stratégies écologiques des trois espèces de termites arboricoles

Au terme de cette recherche, nous sommes en mesure de préciser les stratégies écologiques des trois espèces présentes dans les cocoteraies de Nouvelle-Guinée.

M. biroi

M. biroi colonise rapidement le milieu par de nombreuses petites colonies qui en 3½ ans peuvent occuper plus de 60% des arbres présents. *M. biroi* apparaît comme une espèce pionnière capable de se propager rapidement et à longue distance. Les colonies comportent un ou plusieurs nids, en général répartis sur un à trois arbres. Seul un de ces nids comporte une cellule royale contenant les sexués: dans 84% des colonies un couple d'imagos. En cas de disparition des sexués primaires, des néoténiques se développent à partir de nymphes ou d'ouvriers. La faible proportion de nids de *M. biroi* avec des sexués secondaires (16%) dans des plantations de plus de 30 ans suggère que les sexués primaires ont une longue durée de vie ou, alternativement, que la plupart des colonies ont une durée de vie relativement courte et sont remplacées par de nouvelles fondations par essaimage. Cette dernière hypothèse est supportée par les données sur la dynamique de colonisation (chapitre **2** p.**29**, chapitre **4** p. **68**) et paraît la plus vraisemblable. La mort d'un nid contenant les sexués peut être due à une attaque du nid par une espèce compétitrice ou par certaines fourmis à nids arboricoles. Dans de telles circonstances, une possibilité de survie de la colonie existe par l'apparition de sexués secondaires dans un nid satellite mais n'est apparemment pas fort fréquente.

Les nids de *M. biroi* sont peu épais et leur isolation thermique est faible. Lorsque le nid est ensoleillé, la température en surface approche 50°C et augmente rapidement au centre où elle peut dépasser 35°C. Le nid joue également un rôle important dans la défense de la colonie. L'alarme chez *M. biroi* est déclenchée par des mouvements d'oscillation rapide des ouvriers et par le mouvement vibratoire vertical (*head-banging*, Stuart 1988) des soldats frappant leur capsule céphalique sur le substrat. Nos observations suggèrent également un recrutement défensif par piste, bien qu'il n'ait pas été démontré expérimentalement. La proportion de soldats chez *M. biroi* représente moins de 3% de l'ensemble des castes (Deligne & Pasteels 1982) et les ouvriers prennent une part active dans les combats. Les orifices de communication entre les chambres du nid sont de faible dimension —ne permettant le passage que d'un seul termite à la fois— et sont facilement obturables par la capsule céphalique des soldats; il s'agit d'une stratégie de défense statique ("*static warfare*", Deligne & Pasteels 1982).

N. princeps

N. princeps privilégie le mode de reproduction par bourgeonnement par rapport à l'essaimage (Roisin *et al.* 1987). L'investissement de cette espèce dans cette forme de reproduction se marque par la présence d'une forme particulière d'ailés à ailes courtes incapables d'essaimer mais prêts à se développer en sexués secondaires (Roisin & Pasteels 1985a). Dans des plantations claires ou standard, *N. princeps* colonise de 2 à 4 arbres. Dans des conditions favorables, c'est-à-dire dans les milieux denses, riches en sites de nidification et en nourriture, *N. princeps* développe de très grands nids polygynes (Roisin & Pasteels 1985a) pouvant coloniser jusqu'à 20 arbres. Dans notre échantillonnage, environ 30% des colonies étaient polydômes (chapitre **2**); la multiplication des nids utilisés par une même colonie permet à la fois de maintenir les échanges gazeux et de répartir le poids des nids qui finiraient par crouler de leur support. Un autre avantage est de répartir la population de neutres afin de devoir parcourir une distance réduite jusqu'aux sources de nourriture ou aux zones de combats. Exceptionnellement des supercolonies apparaissent, vraisemblablement par bourgeonnement intense d'une colonie ou peut-être par fusion de colonies peu ou pas antagonistes. En de telles circonstances *N. princeps* peut devenir écologiquement dominante et former des populations très importantes (le volume cumulé des 134 nids de la supercolonie observée dans la parcelle XVI atteignait 5957 dm^3). Former de très grandes colonies polydômes permet d'exploiter plus complètement le milieu, de facilement extirper ou annexer les colonies voisines et probablement de mieux se défendre contre les prédateurs. Dans de tels systèmes de nombreuses reines sont produites et fournissent une importante quantité d'oeufs. La longévité de telles supercolonies est théoriquement très longue puisque les sexués qui disparaissent sont facilement remplacés par des adultoïdes (Roisin & Pasteels 1986a). Dans de tels systèmes, la variabilité génétique au sein de la population va diminuant par accroissement de la consanguinité. Les supercolonies de termites comme de fourmis (Higashi 1979, Chérix *et al.*

1980) se développent dans des milieux uniformes et étendus (Hölldobler & Wilson 1977). Néanmoins, même dans de telles conditions de stabilité et d'uniformité, le modèle théorique de Hamilton & May (1977) prédit qu'une colonie a toujours intérêt à se disperser à longue distance et, de fait, *N. princeps* combine un mode de reproduction à courte (bourgeonnement) et à longue distance (essaimage) (Roisin & Pasteels 1986a, c).

Le microclimat interne du nid ellipsoïdal de *N. princeps* est tamponné par rapport aux variations du milieu extérieur. A l'ombre, la température au centre du nid fluctue entre 29.0°C et 31.6°C et est généralement plus élevée que celle du milieu extérieur vraisemblablement suite à la chaleur dégagée par le métabolisme des termites.

Les soldats nasutis constituent plus de 10% de l'ensemble des castes (Deligne & Pasteels 1982, Haverty 1977); ils servent d'éclaireurs et sont toujours en première ligne lorsque le nid ou les galeries sont ébréchés. Lorsqu'ils entrent en contact avec un ennemi, ils projettent leur sécrétion défensive composée de monoterpènes et de diterpènes (Dupont *et al.* 1981, Everaerts *et al.* 1988b). Chez *N. princeps* cette sécrétion défensive des soldats a pour effet d'alarmer les ouvriers et de les recruter sur les lieux de combat (Roisin *et al.* 1990) où ils attaquent leurs adversaires en utilisant leurs mandibules. La sécrétion défensive des *Nasutitermes* est une arme efficace contre les fourmis de par son action gluante et irritante (Eisner *et al.* 1976, Everaerts 1988). Les fourmis inquilines ne se retrouvent d'ailleurs que dans 5% des nids de *N. princeps*, soit deux fois moins fréquemment que chez *M. biroi* qui ne dispose que d'une arme mandibulaire. Néanmoins, face à de très fortes populations de fourmis, telles celles de *Crematogaster* sp. A, l'abondance de *N. princeps* diminue dans des proportions identiques à celle constatée pour *M. biroi*. Le nid de *N. princeps* est constitué de larges chambres qui permettent une bonne diffusion des signaux chimiques et un recrutement rapide des soldats en cas d'invasion; il s'agit d'une stratégie de défense dynamique ("*movement warfare*" Deligne & Pasteels 1982). Par ailleurs, face à *M. biroi*, la stratégie de *N. princeps* n'est pas uniquement défensive mais aussi offensive, pratiquant un encerclement du nid de *M. biroi* et pénétrant dans le nid en en perforant les cloisons —les orifices de communication entre chambres dans le nid de *M. biroi* étant trop étroits pour eux—. Ces attaques sont nécessaires à l'extension territoriale de *N. princeps* dans un milieu déjà largement occupé par *M. biroi*.

N. novarumhebridarum

Les colonies de *N. novarumhebridarum* contiennent toujours un couple d'imagos (Roisin & Pasteels 1987a). La reproduction des colonies se fait uniquement par essaimage.

N. novarumhebridarum est quatre fois plus fréquent sur des arbres morts que sur des arbres vivants (contre 1.6 fois dans le cas de *N. princeps* et 0.7 fois dans le cas de *M. biroi*). Le mode de reproduction par essaimage de *N. novarumhebridarum* apparaît donc bien adapté à l'utilisation des arbres morts qui sont une ressource dispersée et épuisable. Une faible part, moins de 15% des colonies sont constituées de 2 nids. Le remplacement des sexués par des ergatoïdes est possible mais est un événement apparemment rare en nature (Roisin & Pasteels 1987a).

La structure du nid et les moyens de défense de *N. novarumhebridarum* sont similaires à ceux de *N. princeps* à la différence que chez *N. novarumhebridarum* il n'y a pas d'action phéromonale de la sécrétion défensive (cf. annexe **7**). Les colonies de *N. novarumhebridarum* sont de taille plus restreinte que celles de *N. princeps*, colonisant de 1 à 3 arbres dans des plantations claires ou standard et de 2 à 6 dans des plantations denses.

Coexistence des trois espèces antagonistes

Les niches écologiques des trois espèces se chevauchent largement: leur régime alimentaire, leur site de nidification, leur rythme d'activité, et la taille de leurs individus sont similaires ou identiques. En règle générale, *M. biroi* est l'espèce la plus abondante en cocoteraie, quel que soit l'âge de celle-ci (10 à 80 ans), malgré la supériorité des deux *Nasutitermes* lors de combats. Le succès de *M. biroi* dans le milieu tient à son mode de reproduction qui lui permet de coloniser rapidement de nouveaux habitats et de recoloniser rapidement les vides laisssés par *N. princeps*. *N. princeps* ne devient que rarement l'espèce la plus abondante dans le milieu, sans doute parce qu'elle privilégie un mode de reproduction à courte distance (bourgeonnement), requiert des milieux denses pour développer de grandes colonies, est ralentie par la chute des trop gros nids qui croulent sous leur propre poids et se fait devancer dans le milieu par *M. biroi* qui occupe de nombreux sites de nidification. Quant à *N. novarumhebridarum*, sa distribution est conditionnée par la présence de troncs morts.

En conclusion, la coexistence des trois espèces résulte essentiellement des asymétries entre leurs modes de reproduction et de défense. *M. biroi* investit dans la production d'ailés qui colonisent rapidement le milieu tandis que *N. princeps* investit dans l'agressivité et développe ponctuellement de larges colonies capables de bourgeonner. *N. novarumhebridarum* se spécialise dans l'exploitation d'arbres morts, ressource assez rare et éparpillée en cocoteraie mais à laquelle elle accède grâce à un mode de dispersion efficace à longue distance. Le succès de *M. biroi* provient vraisemblablement de son aptitude à coloniser rapidement le milieu par de nombreuses petites colonies.

Importance relative des facteurs écologiques qui déterminent la distribution et l'abondance des termites à nid arboricole en cocoteraie néo-guinéenne.

Deux facteurs diminuent de moitié l'abondance des termites en cocoteraie: une faible densité d'arbres ou la présence d'une forte densité de fourmis à nids arboricoles. L'effet de la structure de l'habitat, à laquelle sont liés l'ensoleillement et la densité de ressources disponibles, se marque également sur le volume des nids de termites qui est plus important dans des plantations denses que dans des plantations standard ou claires. La réponse aux variations de la structure de l'habitat varie apparemment d'une espèce à l'autre: l'abondance de *M. biroi* diminuant surtout dans les plantations claires, l'abondance de *N. princeps* augmentant surtout dans les plantations denses tandis que l'abondance de *N. novarumhebridarum* semble assez constante d'un type de plantation à l'autre. Quant à l'impact des fourmis arboricoles *Crematogaster* sp. A, il ne se marque que très localement dans les cocoteraies qui semblent être pour elles un habitat marginal dans lequel elles sont peu abondantes.

L'abondance des termites est affectée par la compétition intra- et interspécifique. Il est intéressant de noter que c'est dans la parcelle XVI, occupée par une supercolonie de *N. princeps* —autrement dit en l'absence de compétition intraspécifique et en la quasi absence de compétition interspécifique (*M. biroi* occupait seulement 4% des arbres présents)—, que le plus fort taux d'occupation jamais observé, 84% des arbres présents occupés par des termites, a été atteint. La très forte densité de population observée à cette occasion suggère que la capacité portante (K) du milieu est assez élevée et qu'en général la densité de termites observée en cocoteraie est en deçà de K. Dans des parcelles où seule s'exerçait une compétition entre colonies de *M. biroi*, 66 ± 8% des arbres étaient occupés (moyenne ± écart type, n= 4: parcelles en plantation standard où moins de 1% des cocotiers présents étaient occupés par des *Nasutitermes*). Dans des parcelles où les trois espèces étaient présentes dans le rapport moyen 85 : 12 : 3 (*M. biroi* : *N. princeps* : *N. novarumhebridarum*), 53 ± 8% des arbres étaient occupés (n= 9, parcelles en plantation standard et denses). La compétition interspécifique entraîne la disparition de colonies matures de *M. biroi* à proximité des colonies de *N. princeps* tandis que la compétition intraspécifique est atténuée par des mécanismes d’évitement (divergence des pistes) entre colonies antagonistes. La compétition interspécifique apparait donc supérieure à la compétition intraspécifique.

Les fourmis inquilines n’étaient présentes que dans 5-10% des nids et leur présence paraissait opportuniste et/ou ne pas constituer une menace directe pour la population de termite.

Dans le contexte de la plantation de cocotier, l’importance relative des facteurs écologiques qui affectent la distribution et l’abondance des termites apparaît comme suit: (1) structure du milieu (ensoleillement + densité de nourriture et de sites de nidification), (2) compétition interspécifique entre *M. biroi* et *Nasutitermes* spp. (extirpation des *M. biroi*), (3) compétition intraspécifique entre colonies de *M. biroi* (exclusion mutuelle des colonies), (4) prédation locale par les fourmis à nids arboricoles, (5) interférences des fourmis inquilines.

En milieu forestier, des observations préliminaires suggèrent que la pression de prédation doit être plus forte qu’en cocoteraie car les nids de *M. biroi* récoltés en forêt étaient fréquemment envahis partiellement de fourmis. La densité des colonies de termites arboricoles paraît moindre en forêt qu’en cocoteraie et l’on peut supposer que les phénomènes de compétition intra- et inter-spécifiques sont moins intenses dans ces conditions. Des galeries de *M. biroi* envahies par des *N. princeps* ont néanmoins été observées en forêt.

Territorialité des termites à nids arboricoles

Dans des plantations denses les aires de récolte de *N. princeps* peuvent couvrir de larges étendues. Le réseau de galeries qui mène aux troncs et aux sources de nourritures exploitées au sol est partiellement hypogé et partiellement épigé. Certaines galeries épigées sont suffisamment larges pour permettre la circulation simultanée de nombreux individus (Fig. **37**, p. **134**) facilitant le recrutement rapide vers une source de nourriture ou vers un lieu de combat. Des cartographies mensuelles ont révélé que certaines galeries au sol et sur les troncs persistaient plusieurs mois, bien qu’elles restent éventuellement inoccupées de manière passagère (annexe **3** p. **135**). Il est donc possible que les termites n’utilisent, à un moment donné, qu’une partie de leur réseau. A un an d’intervalle, le réseau fluctue sensiblement autour du nid (Fig. **47** p. **143**). Autour des grands nids de *N. princeps* apparaissent des zones inoccupées par des termites arboricoles, vraisemblement suite à la rotation des aires de récolte qui empêche l’établissement d’autres colonies.

L’organisation des réseaux de galeries de *N. novarumhebridarum* est proche de celui de *N. princeps* (Fig. **38** p. **137**) cependant *N. novarumhebridarum* a une propension moindre à étendre son territoire, vraisemblablement parce que ses nids sont moins volumineux (populeux) et qu’un seul tronc mort doit suffir à nourrir l’ensemble de la colonie. La zone inhabitée autour d'un nid de *N. novarumhebridarum* est en conséquence moins étendue qu'autour d'un nid de *N. princeps* (Fig. **11** p. **28**).

Moins de données sont disponibles sur la territorialité de *M. biroi*, son fin réseau de galeries au sol étant très difficile à cartographier. Néanmoins, la densité de colonies de *M. biroi* (entre 25 et 30 colonies/ha) laisse présumer que les réseaux de colonies voisines, bien que s'évitant, sont partiellement interdigités (Fig. **31** p. **88**).

L'agressivité intercoloniale, à l'origine de l'exclusion mutuelle des colonies au niveau des sources de nourriture et des sites de nidification, joue un rôle fondamental dans l'assemblage de la communauté. Une rencontre entre deux colonies antagonistes de même espèce aboutit généralement à la divergence des galeries ou à l'élimination des colonies plus faibles, de manière analogue à celle observée chez *N. corniger* et *N. nigriceps* (Thorne 1982a, Levings & Adams 1984). L'exclusion mutuelle des colonies de termites à nids arboricoles dans les cocoteraies néo-guinéennes aboutit à un assemblage des territoires en mosaïque. Une telle mosaïque de territoires avait déjà été suggérée par Levings & Adams (1984) pour *N. corniger* et *N. nigriceps* en mangrove. Le terme de mosaïque avait été utilisé par ces auteurs par analogie aux mosaïques de fourmis écologiquement dominantes rencontrées dans de nombreux écosystèmes naturels et artificiels dans la région intertropicale (Majer 1993, Adams 1994a). Les conséquences des mosaïques de fourmis et de termites au niveau de la biocénose ne sont pas comparables pour autant. Les fourmis dominantes, par leur prédation, leur association avec certaines espèces mutualistes (homoptères), leur intolérance vis-à-vis de fourmis aux niches écologiques proches, ont un impact très profond sur la composition faunistique et floristique de la biocénose (Leston 1973). L'impact des mosaïques de termites ne concerne que l'abondance et la distribution de ses membres: ainsi dans les cocoteraies de Nouvelle-Guinée nous n'avons pas constaté d'exclusion des termites à nids terrestres par les termites à nids arboricoles; au contraire, dans les mangroves de Panama les *Termes panamaensis* se localisaient dans les lacunes entre les territoires de *Nasutitermes* spp. (Levings & Adams 1984).

Les connaissances actuelles sur les termites à nids arboricoles nous apprennent qu'ils recourent à différentes formes de territorialité: territorialité spatio-temporelle chez *Longipeditermes longipes* (Gray & Dhanarajan 1974), pistes permanentes chez *Hospitalitermes monoceros* (Petch 1913 *in* Gray & Dhanarajan 1974), galeries couvertes persistantes chez *M. biroi*, *N. novarumhebridarum*, *N. polygynus*, *N. princeps*, *N. corniger*, *N. costalis*, *N. nigriceps*, et *N. ephratae* (Mathews 1977, Jones 1980, Thorne 1980, Thorne 1982a, Levings & Adams 1984, Roisin & Pasteels 1986b, Adams & Levings 1987).

L'assemblage et l'extension des territoires de ces espèces construisant des galeries couvertes semblent étroitement liés à leur mode de reproduction, à leur mode de défense (ou d'attaque) et à la taille de leurs colonies. Les territoires des colonies de *M. biroi*, espèce essentiellement monogyne aux colonies de taille modérée et qui présente un système de défense statique, apparaissent interdigités. Les *Nasutitermes* spp. ont, quant à eux, un système de défense dynamique. Il a pu être démontré chez *N. nigriceps* et *N. corniger* que la taille du territoire est corrélée positivement au volume des nids constituant une colonie (Adams & Levings 1987). *N. novarumhebridarum*, toujours monogyne (Roisin & Pasteels 1987a), constitue des colonies de taille modérée, mono- ou parfois dicaliques, et occupe des territoires restreints. Il semble en être de même pour *N. ephratae* également essentiellement monogyne (Thorne 1985b, Becker 1961, Mathews 1977) et aux colonies de taille modérée (Mathews 1977). Chez ces deux espèces, la sécrétion défensive des soldats n'a pas d'action phéromonale (annexe **7**, Maschwitz 1966, Maschwitz & Mühlenberg 1972). D'autres *Nasutitermes* spp. sont fortement polygynes. La polygynie chez ces espèces semble être liée à un mode de multiplication des colonies par bourgeonnement, ainsi qu'exprimé chez *N. princeps*, *N. polygynus*, *N. costalis* et *N. corniger* (Roisin & Pasteels 1985a, b, 1986a, b, Roisin 1987, Thorne 1982c). *N. princeps* maintient par le déplacement des pistes autour du nid principal, une aire de récolte où la colonie a un accès prioritaire mais qui n'est pas défendue en permanence. Le maintien de ce territoire par *N. princeps* est certainement facilité par l'action phéromonale des monoterpènes de la sécrétion défensive de leurs soldats alarmant et recrutant les ouvriers sur les lieux de combat (Roisin *et al.* 1990). Cette action phéromonale de la sécrétion défensive a aussi été démontrée chez *N. costalis* (Vrkoc *et al.* 1978, Traniello 1981). Il est intéressant de noter que la composition monoterpénique chez ces espèces est stable entre colonies alors qu'elle varie chez *N. novarumhebridarum* et *N. ephratae* (Valterová *et al.* 1993, Pasteels *et al.* 1988). Dans certains cas les *Nasutitermes* fortement polygynes et polycaliques forment des supercolonies (*N. princeps*; *N. polygynus:* Roisin & Pasteels 1986b, annexe **8**; *N. corniger*: Levings & Adams 1984 cf. Fig. **2**C p. **5**: 38 nids, Thorne 1982b) dont la plus large jamais observée est la supercolonie de *N. princeps* observée dans la parcelle A2. Lorsqu'ils constituent des supercolonies, les termites arboricoles occupent des territoires absolus, non au moyen de patrouillles circulant à ciel ouvert comme chez les fourmis, mais plutôt par la monopolisation de quasi toutes les sources de nourriture et des sites de nidification, empêchant l'installation et le développement de toute autre colonie.

Résumé

1. Trois espèces de termites à nids arboricoles, *Microcerotermes biroi*, *Nasutitermes princeps* et *N. novarumhebridarum*, sont présentes dans les plantations de cocotiers de Nouvelle-Guinée et représentent, par leur abondance, un des composants majeurs de cet agroécosystème. Les trois termites coexistent dans le milieu, malgré des niches écologiques proches, utilisant le cocotier à la fois comme source de nourriture et comme site de nidification. On n'observe jamais plus d'une colonie de termites arboricoles sur un même arbre, suggérant des phénomènes d'exclusion à la fois intra- et interspécifique.
2. Le but du présent travail était de déterminer comment s'organise localement une communauté de termites à nids arboricoles et en particulier d'identifier: (i) les principaux paramètres écologiques qui déterminent la distribution et l'abondance de ces termites; (ii) les mécanismes qui permettent la coexistence de colonies antagonistes; (iii) la territorialité de ces termites arboricoles. Les plantations de cocotiers sont un milieu privilégié pour une telle étude car elles constituent un habitat à la fois homogène et comportant divers arrangements spatiaux des arbres qui permettent d'évaluer l'influence de la densité des sites de nidification, de la densité de nourriture et du microclimat sur la communauté de termites.
3. Les trois espèces étudiées construisent un ou plusieurs nids sur le tronc duquel part un réseau de galeries couvertes qui parcourt les horizons superficiels du sol, atteignant diverses matières végétales en décomposition et aboutissant à d'autres arbres. Une partie du réseau de galeries parcourt le tronc jusqu'à la cime du cocotier. Les colonies de *M. biroi* occupent en général de 1 à 3 arbres. Les colonies sont dans 84% des cas monogynes et sont couramment polycaliques. Le volume moyen des nids est d'environ 11 dm^3. Les sexués secondaires, dérivés de nymphes ou temporairement d'ouvriers, apparaissent en remplacement ou en supplément des sexués primaires, éventuellement dans un nid satellite (bourgeonnement). Cette espèce a été observé colonisant en moins de trois ans et demi plus de 60% des arbres présents dans une jeune plantation auparavant vierge de termites. *M. biroi* apparaît comme l'espèce pionnière dans le milieu qu'elle colonise rapidement par des essaimages massifs. *N. princeps* construit des nids avec un volume de 49 dm^3 en moyenne mais pouvant atteindre jusqu'à 300 dm^3. Les colonies peuvent être constituées de plusieurs nids toujours sur des arbres différents. Cette espèce privilégie la propagation des colonies par bourgeonnement plutôt que par essaimages (Roisin & Pasteels 1985). Les

colonies de *N. princeps* peuvent coloniser jusqu'à 20 arbres ou même se présenter sous forme de supercolonie: un site exceptionnel a été en effet observé avec 134 nids de *N. princeps* concentrés sur une surface de 3.1 ha et dont le volume cumulé des nids atteignait près de 6000 dm^3. Les nids de *N. novarumhebridarum*, toujours monogynes, sont de 20 dm^3 en moyenne. Les colonies de *N. novarumhebridarum*, sont généralement monocaliques et colonisent de 1 à 6 arbres. La propagation des colonies se réalise uniquement par essaimages (Roisin & Pasteels 1987).

4. Lors de l'expansion de son territoire, *N. princeps* rencontre des *M. biroi* aux sources de nourriture ou aux sites de nidification; des combats s'ensuivent desquels *N. princeps* sort apparemment toujours vainqueur: des nids de *M. biroi* envahis par *N. princeps* étant couramment observé alors que l'inverse ne l'a jamais été. *N. princeps* adopte une stratégie offensive encerclant le nid de *M. biroi* et pénétrant à l'intérieur en perforant les parois des chambres. Le nid de *M. biroi* peut être récupéré par *N. princeps* qui en modifie alors l'architecture en fonction de sa biologie propre. Le nid de *M. biroi* est constitué de chambres communicant par d'étroits orifices ne permettant le passage que d'un termite à la fois et facilement obturés par la capsule céphalique des soldats. Il s'agit d'un mode de défense statique (Deligne & Pasteels 1982). Le nid de *N. princeps* est constitué de larges chambres permettant une diffusion rapide des signaux chimiques. La sécrétion défensive des soldats a un rôle de phéromone de recrutement et d'alarme. *N. princeps* adopte un système de défense dynamique (Deligne & Pasteels 1982). Autour des larges colonies de *N. princeps* apparaissent des zones exemptes de termites arboricoles mais qui présentent souvent des traces du passage de *N. princeps* qui, par un réseau de galeries assez étendu et fluctuant, déloge les colonies de *M. biroi* adjacentes et empêche le développement de toute fondation. *N. novarumhebridarum* est également capable d'envahir les nids de *M. biroi* mais a une propension moindre à étendre ses colonies que *N. princeps*. Son nid est d'architecture similaire à celui de *N. princeps* mais la sécrétion défensive des soldats n'a pas de rôle phéromonal. Il est intéressant de noter que la fraction monoterpénique de la sécrétion défensive responsable de l'action phéromonale est stable d'une colonie à l'autre chez *N. princeps* alors qu'elle est variable chez *N. novarumhebridarum* (Pasteels *et al.* 1988).
5. Les termites à nids arboricoles occupent avec leurs nids et galeries, en moyenne la moitié des arbres dans les cocoteraies de Nouvelle-Guinée. L'espèce la plus abondante est *M. biroi* qui est observée sur 80% des cocotiers occupés par un termite arboricole, suivie de *N. princeps* (14%) et de *N. novarumhebridarum* (6%).

6. La structure du milieu (hauteur et densité d'arbres par unité de surface) affecte la distribution et l'abondance des termites à nids arboricoles, vraisemblablement suite aux variations des conditions d'ensoleillement et de disponibilité en nourriture qu'elle entraîne. Si d'une manière générale le volume des nids des trois espèces augmente avec la densité du milieu, des réponses spécifiques s'observent. L'abondance de *M. biroi* peut diminuer de 66% dans les milieux les moins denses, probablement parce que l'ensoleillement direct entraîne des températures trop élevées au sein de ses nids. Quant aux nids des deux *Nasutitermes*, ils sont de par leur architecture mieux isolés et leur température interne est tamponnée par rapport aux variations de température extérieure. Les très larges colonies de *N. princeps* ne se rencontrent que dans les milieux les plus denses où elles trouvent en abondance la nourriture et les sites de nidification favorables à leur développement. L'abondance des *N. novarumhebridarum* semble assez constante quel que soit le type de milieu. *N. novarumhebridarum* est quatre fois plus fréquent sur des arbres morts que sur des arbres vivants.
7. L'agressivité entre colonies de termites à nids arboricoles de même espèce a été observée dans 66-79% des colonies confrontées expérimentalement et semble à la fois constante dans le temps et peu liée au degré de parenté génétique entre colonies adverses. La rencontre de pistes provenant de colonies antagonistes entraîne des combats mais débouche sur l'évitement plutôt que l'anéantissement de l'adversaire. La fusion de pistes entre colonies non agressives de *N. princeps* ou de *N. novarumhebridarum* a été observée en conditions semi-naturelles. Dans le cas de *N. princeps* cette fusion pourrait être, parallèlement au bourgeonnement intense d'une colonie, l'un des modes d'apparition de supercolonies. De plus la fusion de colonies ouvre la possibilité de croisement intercolonial en l'absence de vol nuptial (au cas où des individus provenant d'une autre colonie se développeraient en sexués de remplacement). Chez *N. novarumhebridarum*, la fusion en conditions naturelles est très improbable étant donnée la dispersion des colonies liée à la présence de troncs morts.
8. Les termites à l'intérieur de leurs constructions sont en général bien protégés des prédateurs. Deux types de fourmis sont cependant susceptibles d'interférer avec les termites arboricoles. Les fourmis inquilines d'abord qui peuvent cohabiter plusieurs années avec les termites, vivant dans des parties du nid ou des galeries séparées. Dans certains cas ces fourmis finissent par envahir totalement le nid. Néanmoins, en moyenne, les fourmis inquilines ne sont présentes que dans 10% des nids de *M. biroi* et dans 5% des nids de *N. princeps*. Le second type de fourmis sont les fourmis à nids arboricoles dont certaines

(*Crematogaster* sp. A) sont présentes par foyers dans les plantations et, dans ce cas, diminuent de moitié l'abondance des termites. Ces concentrations de fourmis à nids arboricoles sont peu fréquentes dans les plantations de cocotiers qui semblent être pour elles un habitat marginal.

9. La coexistence des trois espèces résulte essentiellement des asymétries entre leurs modes de reproduction et de défense. *M. biroi* investit dans la production d'ailés qui colonisent rapidement le milieu tandis que *N. princeps* investit dans l'agressivité et développe ponctuellement de larges colonies capables de bourgeonner. *N. novarumhebridarum* se spécialise dans l'exploitation d'arbres morts, ressource assez rare et éparpillée en cocoteraie mais à laquelle elle accède grâce à un mode de dispersion efficace à longue distance. Le succès de *M. biroi* provient vraisemblablement de son aptitude à coloniser rapidement le milieu par de nombreuses petites colonies. Malgré sa vulnérabilité vis-à-vis de ses compétiteurs, son mode de reproduction efficace lui permet de les devancer dans les habitats nouvellement disponibles ou même de reconquérir les territoires abandonnés par ses ennemis. *N. princeps*, malgré son agressivité, supplante rarement *M. biroi*, même dans des plantations âgées de plus de 40 ans. Plusieurs explications peuvent être trouvées à cela: (1) *N. princeps* est un piètre colonisateur par essaimages et doit fonder des sociétés dans un milieu déjà envahi par une espèce hostile (2) le tronc cylindrique du cocotier n'est pas un support approprié pour les très gros nids qui finissent par crouler sous leur propre poids (3) alors que les ressources d'un seul arbre semblent suffir à subvenir aux besoins d'un nid de *M. biroi*, *N. princeps* pour développer de grandes colonies semble nécessiter une haute densité de nourriture qui ne se rencontre que dans les milieux denses.
10. Dans le contexte de la plantation de cocotier, l'importance relative des facteurs écologiques qui affectent la distribution et l'abondance des termites apparaît comme suit: (1) structure du milieu (ensoleillement + densité de nourriture et de sites de nidification), (2) compétition interspécifique entre *M. biroi* et *Nasutitermes* spp. (extirpation des *M. biroi*), (3) compétition intraspécifique entre colonies de *M. biroi* (exclusion mutuelle des colonies), (4) prédation locale par les fourmis à nids arboricoles, (5) interférences des fourmis inquilines.
11. L'agressivité intercoloniale, à l'origine de l'exclusion mutuelle des colonies au niveau des sources de nourriture et des sites de nidification, joue un rôle fondamental dans l'assemblage de la communauté. L'exclusion mutuelle des colonies, à la fois inter- et intraspécifiquement, aboutit à un assemblage des territoires en mosaïque. La densité de colonies de *M. biroi* (entre 25 et 30 colonies/ha) et des expériences de rencontres

internidales suggèrent que les réseaux de galeries provenant de colonies voisines, bien que s'évitant, sont partiellement interdigités. *N. novarumhebridarum* occupe des territoires restreints aux abords du tronc mort exploité. *N. princeps* maintient par le déplacement des pistes autour du nid principal, une aire de récolte où la colonie a un accès prioritaire mais qui n'est pas défendue en permanence. La territorialité de ces termites arboricoles apparaît analogue aux pistes permanentes de fourmis. Dans certains cas cependant, *N. princeps* forme des supercolonies et occupe alors un territoire absolu maintenu à partir d'un système de nids décentralisés qui monopolise tous les sites de nourriture et de nidification et empêche l'établissement de toute autre colonie.

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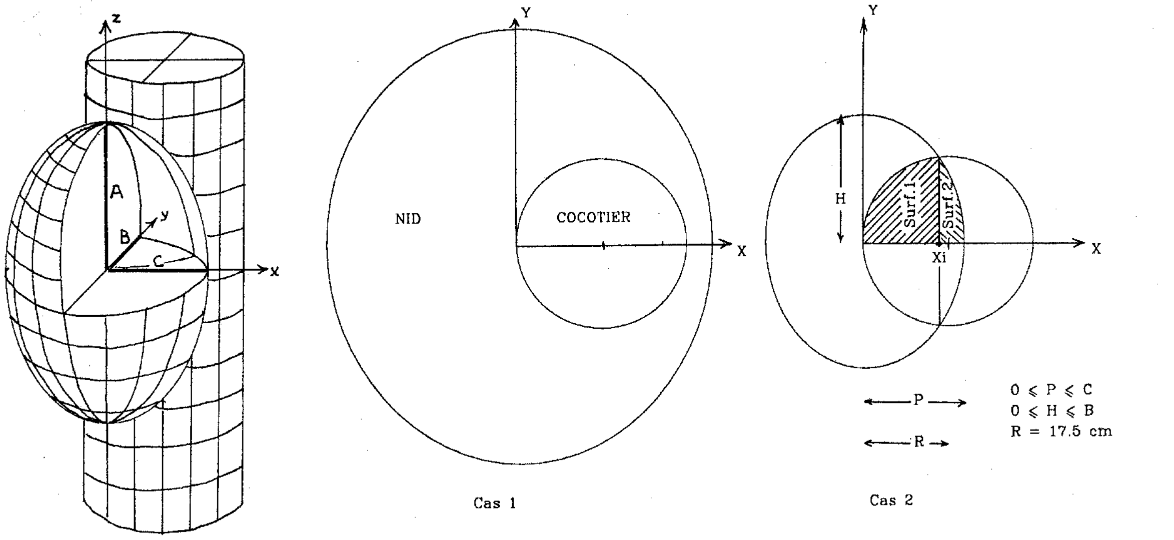
Annexes

Nid de *Microcerotermes biroi* sculpté.
(village de Nubia, Nouvelle-Guinée)

Annexe 1: Algorithmes de calcul du volume des nids

volume des nids de *Nasutitermes*

Ainsi que l'illustre la Fig. 34, les nids de *Nasutitermes* peuvent être assimilés à un ellipsoïde de révolution centré sur l'écorce du tronc du cocotier.



↑ vue tridimensionelle du nid de *Nasutitermes* perché sur un cocotier

↑Section, dans le plan XY, à une hauteur z où le nid entoure le tronc du cocotier (cas 1)

↑ Section, dans le plan XY, à une hauteur z' où le nid n'entoure pas le tronc du cocotier (cas 2)

Figure 34: nid de *Nasutitermes* perché sur un tronc de cocotier: vue dans l'espace et coupe transversale.

Volume de l'ellipsoïde plein

Vplein = 4/3 . π . A . B . C
où A, B, C sont les axes de l'ellipsoïde et π =3.14159

Calcul du volume de l'intersection entre l'ellipsoïde et le cylindre

La méthode consiste à calculer le volume de fines tranches horizontales de l'intersection et ensuite de les sommer selon l'axe vertical. Le volume des fines tranches se calcule en multipliant la surface de l'intersection obtenue pour un z donné par la hauteur de la tranche.

Pour un z donné,
- si le nid entoure le tronc du cocotier, l'intersection est un cercle de surface (π . R^2). **(cas 1)**
- si le nid n'entoure pas le tronc du cocotier, l'intersection est composée de deux aires , l'une sous-tendue par un cercle (tronc) et l'autre par une ellipse (nid). Les surfaces peuvent se calculer par intégrale à condition de connaître l'abscisse du point d'intersection Xi entre le cercle et l'ellipse. **(cas 2)**.

Détermination du point d'intersection Xi:

L'équation de l'ellipse à un niveau z donné (z compris entre 0 et A) est: $(x^2/P^2)+(y^2/H^2)=1$ ce qui équivaut à $y=H.\sqrt{1-(x^2/P^2)}$ **(1)**

P et H sont les axes de l'ellipse pour un z donné et sont compris respectivement entre 0 et C et entre 0 et B en vertu des relations suivantes: P=K.C et H=K.B où
$K=\sqrt{1-(z^2/A^2)}$
[en effet l'équation générale de l'ellipsoïde est: $(x^2/C^2) + (y^2/B^2) + (z^2/A^2) = 1$ et pour y=0, x=P et pour x=0, y=H]

L'équation du cercle à un niveau z donné est $(x-R)^2+y^2=R^2$ ce qui équivaut à
$y=\sqrt{R^2-(x-R)^2}$ **(2)**

(1)=(2) $\Rightarrow$ $(H^2/P^2-1).x^2+(2.R).x-h^2=0$; la résolution de cette équation du second degré permet de calculer $Xi=[-R\pm\sqrt{(R^2+H^2.((H^2/P^2)-1)}]\ /\ [(H^2/P^2)-1]$

Une étude de signe permet de déterminer les cas où l'intersection est
- un cercle: cas 1 : solutions imaginaires si

- P=H & H>(2.R)
- $P\neq H$ & $(R^2+H^2.((H^2/P^2)-1))<0$
- $P\neq H$ & $(R^2+H^2.((H^2/P^2)-1))\geq 0$ & X>(2.R)

- composée de deux aires (deux fois Surf.1+Surf.2): cas 2 : solutions réelles (dans tous les autres cas).

Détermination de la surface sous le cercle:
intégrale de (2) de 0 à Xi =
$Surf1=[(R^2/2).ACOS((R-Xi)/R)] - [(R-Xi).\sqrt{(2.R.Xi)-(Xi^2/2)}\ ]$
où ACOS= arc cosinus (en radians).

Détermination de la surface sous l'ellipse:
intégrale de (1) de Xi à P =
$Surf2 = [\ (B.K^2.C)/2]\ .\ [(\pi/2) - ASIN(Xi/(K.C) - (Xi/(K.C).\ \sqrt{1-(Xi/(K.C))^2}]$
où ASIN = arcsinus en radians

Cas 1: Surface de l'intersection (pour Xi imaginaire): $Surfinter=\pi.R^2$

Cas 2: Surface de l'intersection (pour Xi réel): Surfinter=2.(Surf1+Surf2)

Volume de l'intersection= (2 . Surfinter . hauteur de la tranche)

La hauteur de la tranche utilisée lors des calculs est de 1 cm.

Volume du nid de Nasutitermes:

Volume du nid = (Volume de l'ellipsoïde plein - Volume de l'intersection)

volume des nids de *Microcerotermes biroi*

Ainsi que l'illustre la Fig. 35, le nid de *M. biroi* est assimilé à un secteur de cylindre creux.

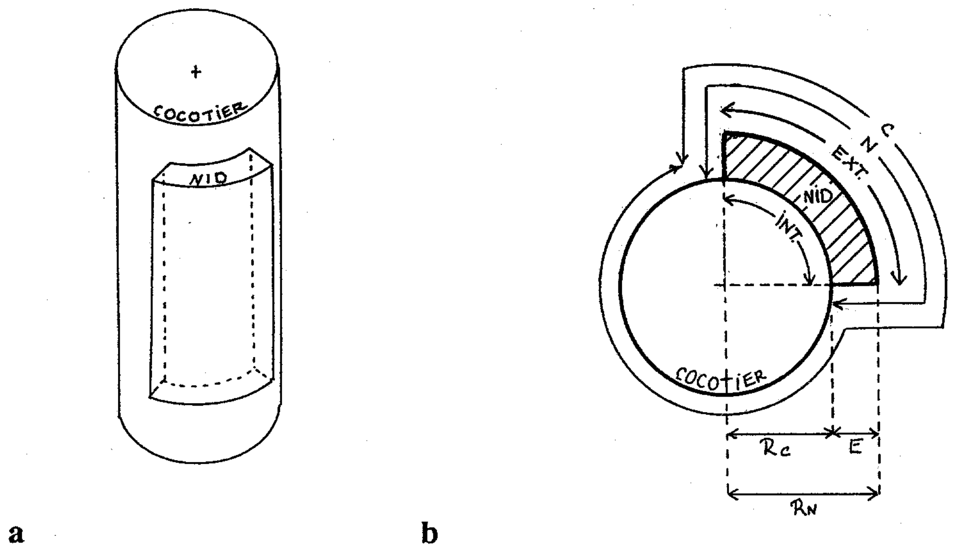


Figure 35: nid de *M.biroi* assimilé à un secteur de cylindre creux (pour notations voir texte). **a**: vue tridimensionnelle du nid sur le cocotier. **b:** vue en coupe.

Variables connues (mesurées sur le terrain):
C: circonférence du tronc et du nid
E: épaisseur du nid
N: longueur du pourtour du nid
H: hauteur du nid

Variables déduites:
Rc: rayon du cocotier
Rn: rayon du nid (distance du centre du cocotier à la surface extérieure du nid).
Ext: arc de circonférence extérieur (surface extérieure du nid)
Int: arc de circonférence intérieur (surface du nid accolée au tronc)
Sect: secteur de cylindre intercepté par le nid

Relations entre variables:
pour $N \neq C$: $Ext = N - 2.E$ (1)
pour $N = C$: $Ext = N$ (1')
$Ext = 2.\pi.(Rc + E).\ Sect$ (2)
$Sect = Int/(2.\pi.Rc)$ (3)
$Rn = Rc + E$ (4)

1. Calcul du rayon du cocotier:

(2) & (3) → $Ext= 2.\pi.(Rc + E). Int/(2.\pi.Rc)$
on en déduit: $Ext= (1 + (E / Rc)).Int$
ou l'équivalent via (1) → $Int= (N - 2.E)/ (1 + (E / Rc))$ (5) cas où $C \neq N$
via (1') → $Int= N/ (1 + (E / Rc))$ (5') cas où $C=N$

$2.\pi.Rc= (C - N) + Int$ (6)
(5) & (6) → $2.\pi.Rc= (C - N) + (N - 2.E)/ (1 + (E / Rc))$ cas où $C \neq N$
(5') & (6) → $2.\pi.Rc= (C - N) + (N - 2.E)/ (1 + (E / Rc))$ cas où $C=N$

on obtient l'équation du second degré:
- cas où $C \neq N$ $2.\pi.Rc^2 + (2.\pi.E - C + 2. E). Rc - E. (C - N) = 0$
- cas où $C=N$ $2.\pi.Rc^2 + (2.\pi.E - C). Rc - E. (C - N) = 0$

ayant deux solutions, seule la positive nous intéresse:
$Rc= (- b+ \sqrt{b^2-4.a.c}) / 2.a$

où $a = 2.\pi$
$b = 2.\pi.E - C + 2. E$ (cas où $C \neq N$)
$b = 2.\pi.E - C$ (cas où $C=N$)
$c = - E. (C - N)$

2. Secteur de tronc intercepté par le nid:

$Sect= Ext / 2.\pi.Rn$
(4) →
$Sect= Ext / (2.\pi. (Rc + E))$
avec $Ext= N - 2.E$ (cas où $C \neq N$)
avec $Ext= N$ (cas où $C=N$)

3. Volume du nid de *M.biroi*:

$VOL= \pi. (Rn^2 - Rc^2). H. Sect$

Annexe 2: Exploitation des ressources alimentaires

N. princeps, *N. novarumhebridarum* et *M. biroi* se nourrissent des mêmes matières végétales telles que palmes mortes encore attachées au cocotier ou tombées au sol, coir des noix, inflorescences mortes ... La Fig. 36 montre l'exploitation typique de matières végétales sur le sol par *N. princeps* dont la photo d'une galerie épigée est présentée en Fig. 37. *N. novarumhebridarum* et *M. biroi* ont un régime alimentaire et des réseaux de galeries similaires; cependant les galeries de *M. biroi* sont plus étroites que celles des *Nasutitermes*. Aucune des espèces ne s'attaque à des cocotiers vivants, probablement en raison de la dureté de leur bois (Zenker *et al.* 1968).

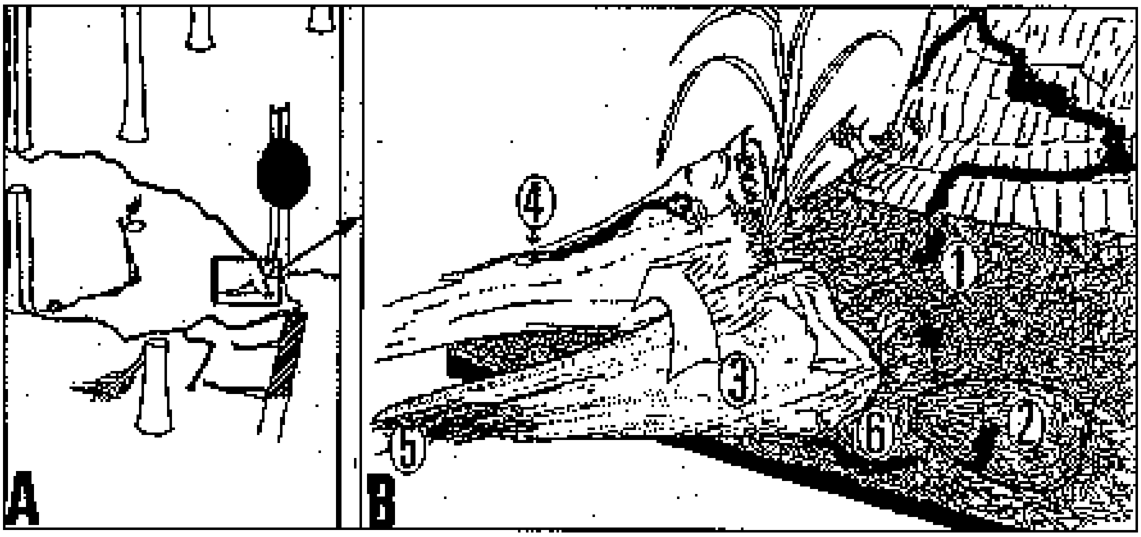


Figure 36. Réseau des galeries principales (A) et exploitation de la nourriture (B) par *N princeps.* Quittant le nid, des galeries pénètrent dans l'entrelacis de radicelles du cocotier ①. Elles atteignent des matières végétales mortes telles une noix avortée ② ou une palme ③. Les galeries parcourent la source de nourriture dans laquelle les termites pénètrent par des orifices creusés dans le plancher des galeries ④ par lesquels ils accèdent à d'autres galeries minées dans la source de nourriture ⑤. Les sources de nourriture sont souvent connectées par des galeries épigées ⑥.

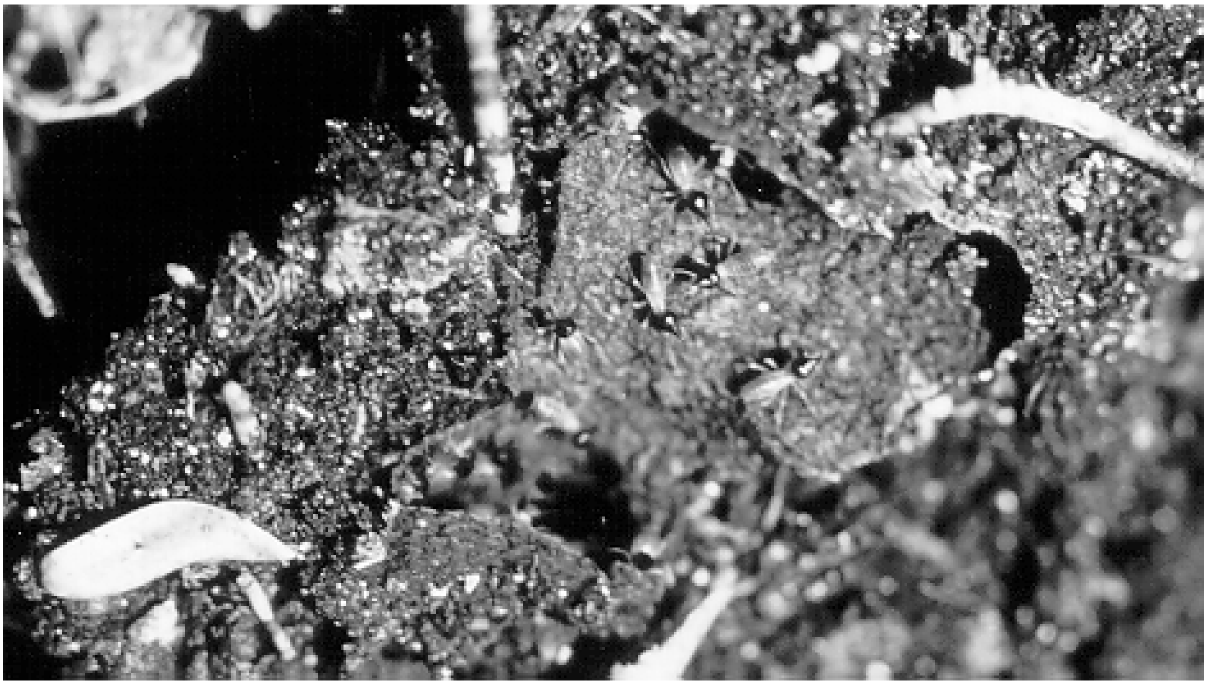


Figure 37: Galerie épigée de *N. princeps*. Des soldats en alerte patrouillent autour de la brèche.

Annexe 3: Réseaux de galeries au sol

Méthode

Dans la parcelle A2, une sous-parcelle incluant 8 cocotiers a été délimitée. Trois nids d'espèces différentes s'y côtoient. Une étude de la localisation des autres nids autour de la sous-parcelle permet d'affirmer qu'en son sein les galeries au sol de *N. princeps* sont issues du nid de coordonnées (colonne: 19, ligne: 17) (volume: 69 dm^3), que celles de *M. biroi* sont issues de (22,16) (4 dm^3). Les galeries de *N. novarumhebridarum* sont issues de (21,17) (28 dm^3), à l'exception de celles dans un rayon de 4 m autour de (22,17) qui proviennent de (22,18) —un nid proche et antagoniste—. L'arrangement spatial des cocotiers est en triangle équilatéral. Chaque arbre est distant en moyenne de 8,5 mètres. Des piquets, 300 au total, ont été disposés tous les 85 cm et selon un schéma en triangle équilatéral, pour faciliter la cartographie des galeries. Lors de l'installation de l'essai la strate herbacée a été coupée à ras. Les palmes et autres matières végétales mortes de cocotiers jonchant le sol ont été perturbées le moins possible. Une cartographie détaillée des matières végétales au sol et de leur infestation par les différentes espèces de termite a été réalisée tous les mois durant 3 mois. Quelques observations intermédiaires ont aussi été réalisées ponctuellement. Les palmes, inflorescences et noix consommées par les termites, ainsi que leurs galeries au sol, ont été marquées par de la peinture acrylique afin de mieux en suivre la colonisation.

Résultats

La figure 38 représente le réseau de galeries au sol 1 mois (Fig. 38A), 2 mois (Fig. 38B) et 3 mois (Fig. 38C) après l'installation de l'essai. Pour les besoins de la représentation graphique chaque parallélogramme élémentaire de 85 cm de côté a été subdivisé en 9 sous-unités égales (parallélogrammes de 28.3 cm de côté). Lorsque des termites arboricoles ont été observés dans la sous-unité, un symbole y a été placé sur la figure 38 (rond pour *N. princeps*, triangle pour *N. novarumhebridarum*, carré pour *M. biroi*). La configuration réelle du terrain, jonché de matières végétales mortes provenant du cocotier est représentée à la Fig 38C'. Malgré toutes les précautions prises pour déranger le moins possible le terrain, le fait que la strate herbacée ait été rabattue a provoqué une sécheresse au niveau du sol qui s'est atténuée ensuite avec la repousse de l'herbe. Les observations après un mois correspondent donc à celles d'un milieu encore perturbé par l'installation du dispositif.

Les galeries couvertes au sol longent généralement des organes morts tombés au sol, en particulier les longues palmes des cocotiers. Les discontinuités dans les réseaux présentés en Fig. 38 résultent de la difficulté de suivre les galeries une fois qu'elles quittent une source de nourriture, d'autant que certaines connections semblent être souterraines. Nous pouvons constater que le réseau de galeries au sol est d'autant plus grand que la colonie est volumineuse (populeuse). Certains organes jonchant le sol apparaissent être consommés pendant au moins 3 mois, tandis qu'une partie du réseau fluctue pendant le même lapse de temps. Des observations intermédiaires aux observations mensuelles ont révélé que certaines sources de nourriture étaient passagèrement abandonnées.

Des rencontres intercoloniales ont pu se produire durant les trois mois d'observation. Le cocotier (20,17) colonisé initialement par des galeries arboricoles de *N. novarumhebridarum* (Fig. 38A) s'est vu abandonné par cette espèce (Fig. 38B&C), peut-être suite à la progression de *N. princeps* à proximité de cet arbre. Quant aux *N. novarumhebridarum*, ils ont atteint le cocotier où se trouvait le nid de *M. biroi* sans toutefois les en déloger (Fig. 38B&C). Les *N. novarumhebridarum* ont même récupéré des galeries qui étaient précédemment occupées par des *M. biroi*. Nous n'avons pas pu observer si cette colonisation secondaire s'est faite de manière active (combats avec *M. biroi*) ou passive (abandon préalable de *M. biroi*). Dix-huit mois plus tard, en mai 1992, le nid de *M. biroi* avait disparu et l'arbre portait des vestiges de galeries de *N. princeps* qui pourraient être responsable de la mort du nid de *M. biroi.*

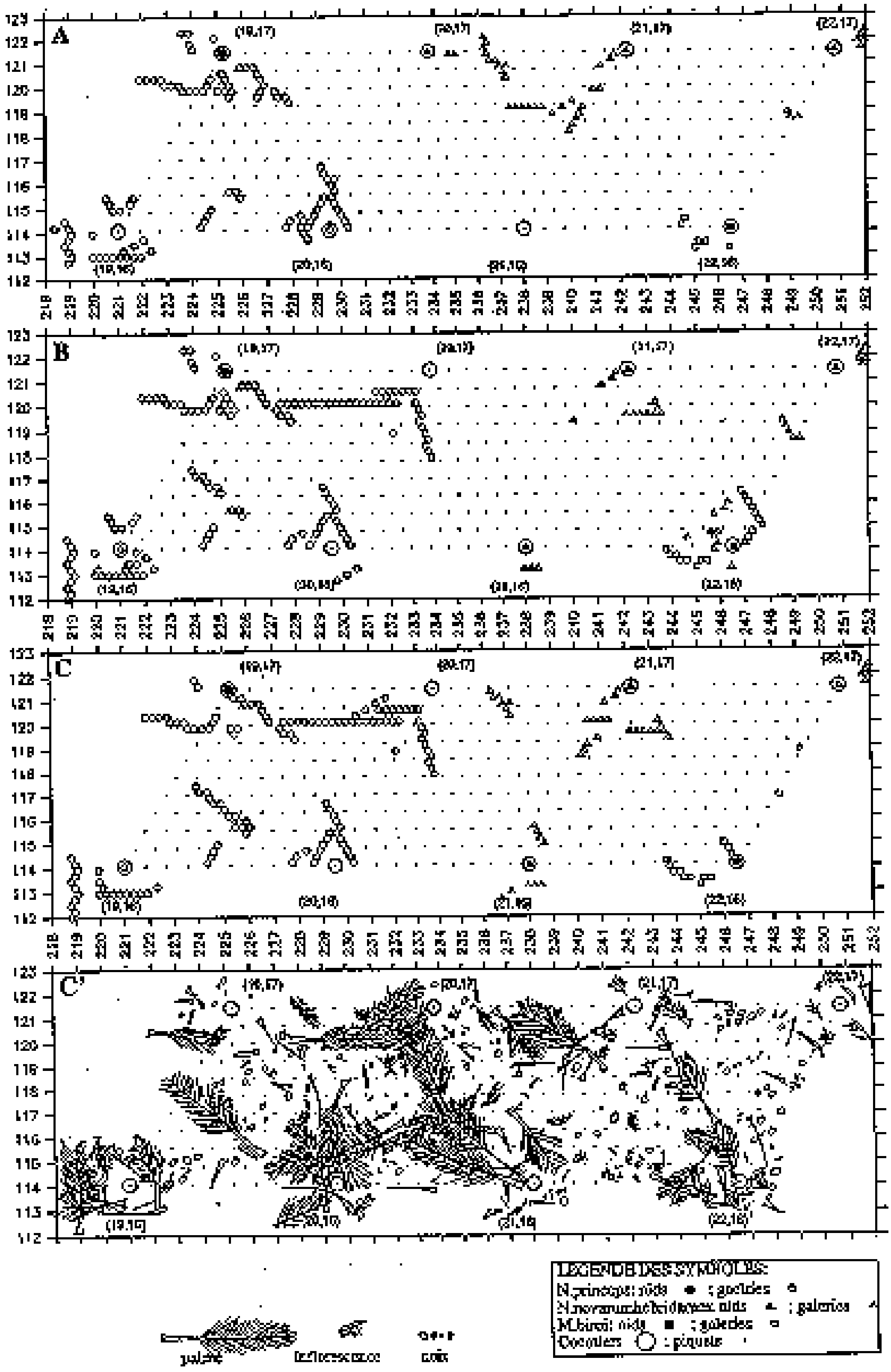


Figure 38: Evolution du réseau de galeries au sol. A-B-C: situtations observées à un mois d’intervalle. C’: configuration réelle du terrain joché de palmes, d’inflorescences et de noix de coco. Axes distances en mètres.

Annexe 4: Données climatiques

Précipitations et saisons

Les précipitations ont été suivies depuis 1978 sur Laing Island (Bouillon *et al.* 1986, Claereboudt *et al.* 1989). Le climat est de type tropical humide. Comme on peut le constater sur la Fig. 39, la saison des pluies s'étend de novembre à avril et la saison sèche de mai à octobre. Une petite saison sèche, dans la saison des pluies, se présente en janvier/février. Ces périodes durent environ 3 semaines. La pluviosité moyenne annuelle est de l'ordre de 1600 mm (moyenne 1978-1993). Les précipitations mensuelles moyennes sont de 233 mm en saison humide et il y pleut en moyenne 13 jours par mois (durant la période 1980-83: Bouillon *et al.* 1986). Les précipitations mensuelles moyennes sont de 54 mm en saison sèche et il y pleut en moyenne 6 jours par mois.

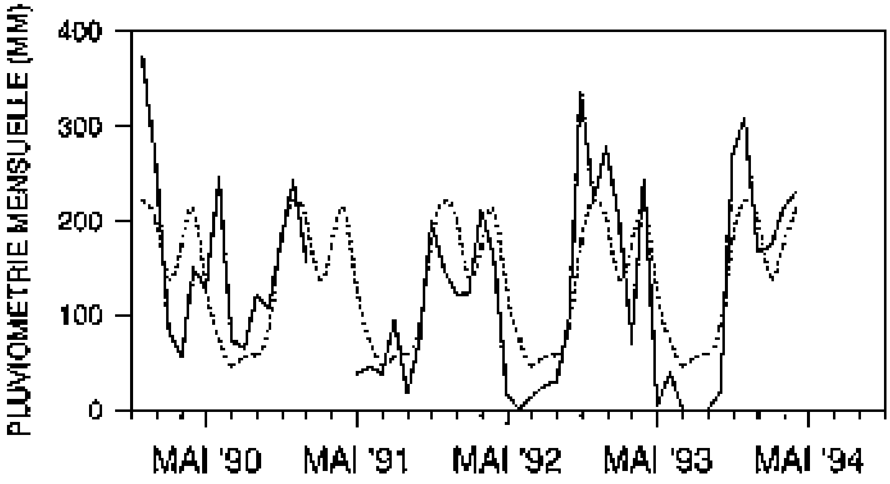


Figure 39: Pluviométrie mesurée à l'île de Laing entre 1990 et 1994 (ligne continue) et moyenne entre 1978 et 1994 (ligne pointillée).

Vents

Pendant la saison humide les vents dominants sont du N.N.O (Fig. 40). Ils sont en général de force modérée mais leur régime est assez irrégulier et ils soufflent quelquefois en fortes rafales. Pendant la saison sèche les vents dominants du S.E. sont très réguliers et assez forts, pouvant atteindre jusqu'à 7 Beaufort (Bouillon *et al.* 1986). Typiquement, les vents se lèvent en fin de matinée et atteignent leur maximum en fin d'après midi. Ils tombent en milieu de nuit. Deux périodes de transition se présentent en fin de saison humide et en fin de saison sèche: en avril, il y a très peu de vents et en octobre-novembre les vents sont variables NO ou SE.

Température et humidité de l'air

La température et l'humidité de l'air sous abri météorologique ont été mesurées par Bouillon et ses collaborateurs (1986) sur Laing Island. La température au cours de l'année est assez uniforme, comprise en moyenne entre 24.5°C et 32.5°C (Fig. 40). La température atmosphérique moyenne est de 28.7°C. Des extrêmes de 22°C —lors de nuits pluvieuses— ou de 34°C à midi —durant des périodes très ensoleillées et en l'absence de vents— sont quelquefois observés. L'humidité relative de l'air atteint ses valeurs maximales la nuit (moyenne annuelle: 97%) et minimales à midi (moyenne annuelle 79%) (Fig. 40). Les minima ont tendance à s'élever et les valeurs maxima à diminuer en saison sèche suite à l'évaporation et aux forts vents de S.E. chargés d'humidité et d'embruns.

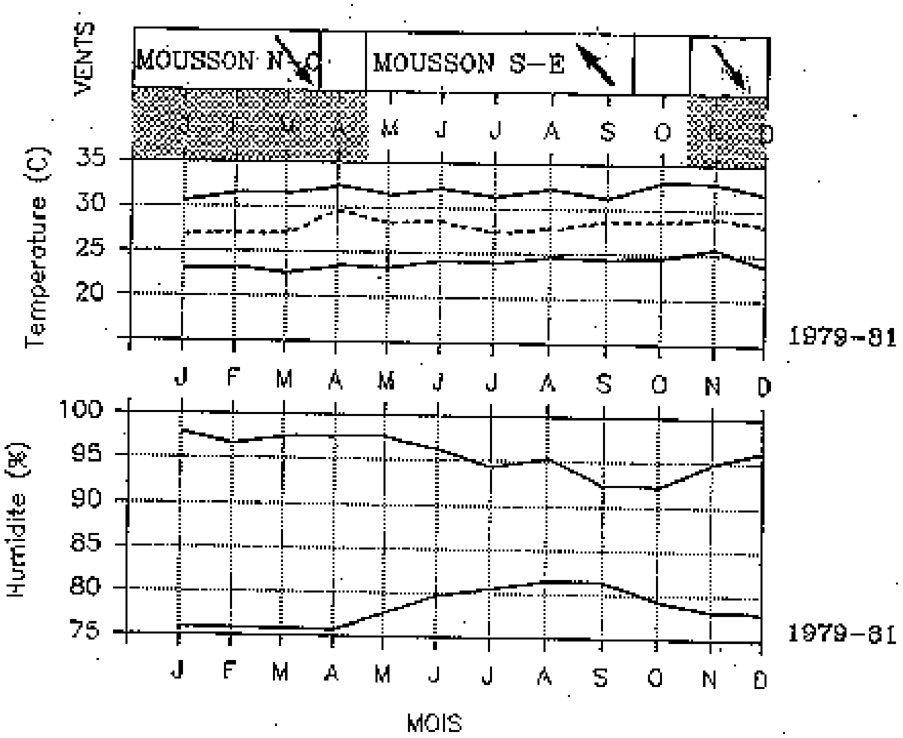
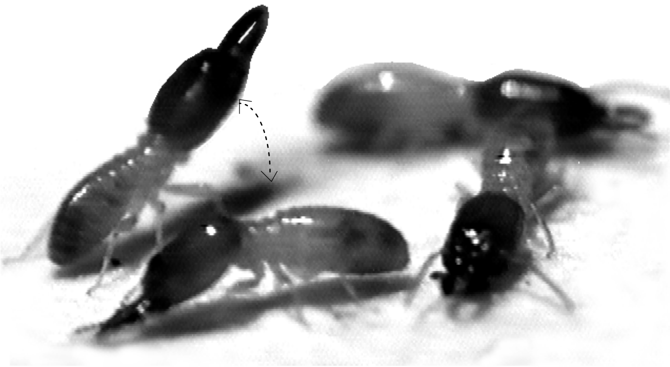


Figure 40: Climat mesuré à l'île de Laing: vents, température et humidité relative (maxima absolu, minima absolu et moyenne sur la période 1979-1981) (d'après Bouillon *et al.* 1986).

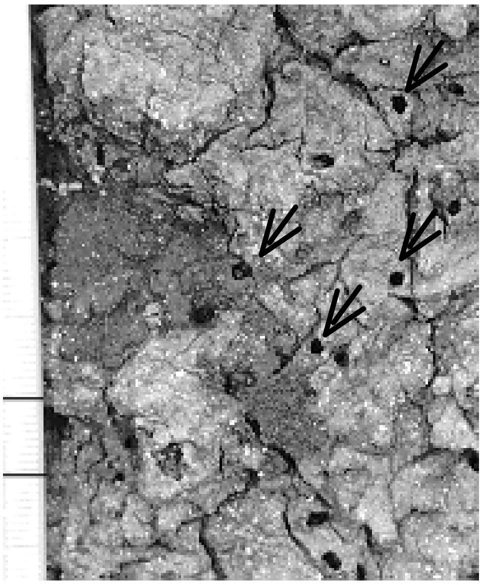
Annexe 5: Attaque d'un nid de *M. biroi* par *N. princeps*



← **Figure 41:** Mouvement vibratoire vertical (*head banging*) de soldats de *M. biroi*. Le soldat en haut à gauche a redressé sa capsule céphalique prêt à la frapper sur le substrat, à l'instar de l'individu en bas à gauche. Observations en laboratoire (image vidéo digitalisée).

← **Figure 42:** Tronc de cocotier couvert de cadavres (points clairs) de *M. biroi* et de *N. princeps* au bas d'un nid de *M. biroi* attaqué et témoignant de combats hors du nid.

↓ **Figure 43:** orifices existant à la surface des nids de *M. biroi*. Les 2 traits sont distants d'1cm.



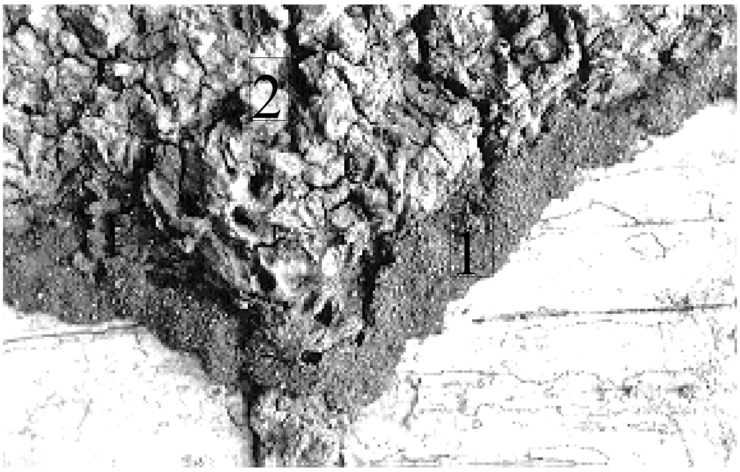


Figure 44: Galeries de *N. princeps* ① entourant le nid de *M. biroi* ② (détail du bas du nid de *M. biroi*).

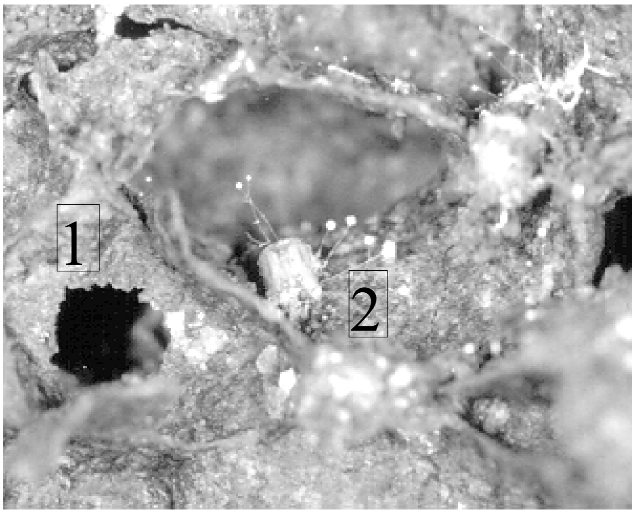


Figure 45: Détail d'une chambre du nid de *M. biroi* attaqué par *N. princeps* avec ① une paroi perforée par *N. princeps* et ② la capsule céphalique d'un soldat de *M. biroi* tué.

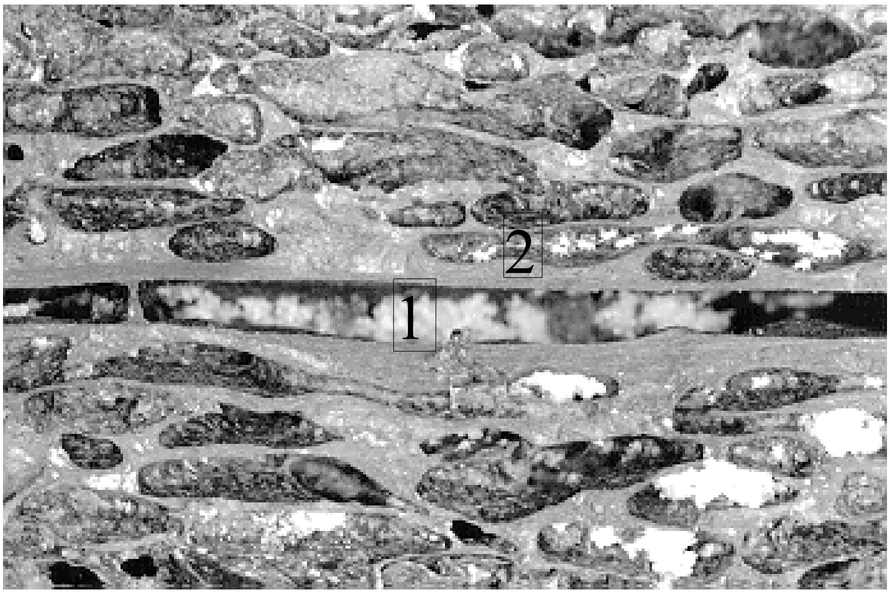


Figure 46: Cellule royale d'un nid de *M. biroi* attaqué par *N. princeps*, dernier retranchement auquel a été trouvé des *M. biroi* vivants après plus d'un semaine de combats. Remarquer: ① les oeufs dans la loge royale et ②les jeunes larves dans les loges avoisinantes. Les sexués n'ont pas été retrouvés.

Annexe 6: Dynamique des réseaux de galeries de *N. princeps*

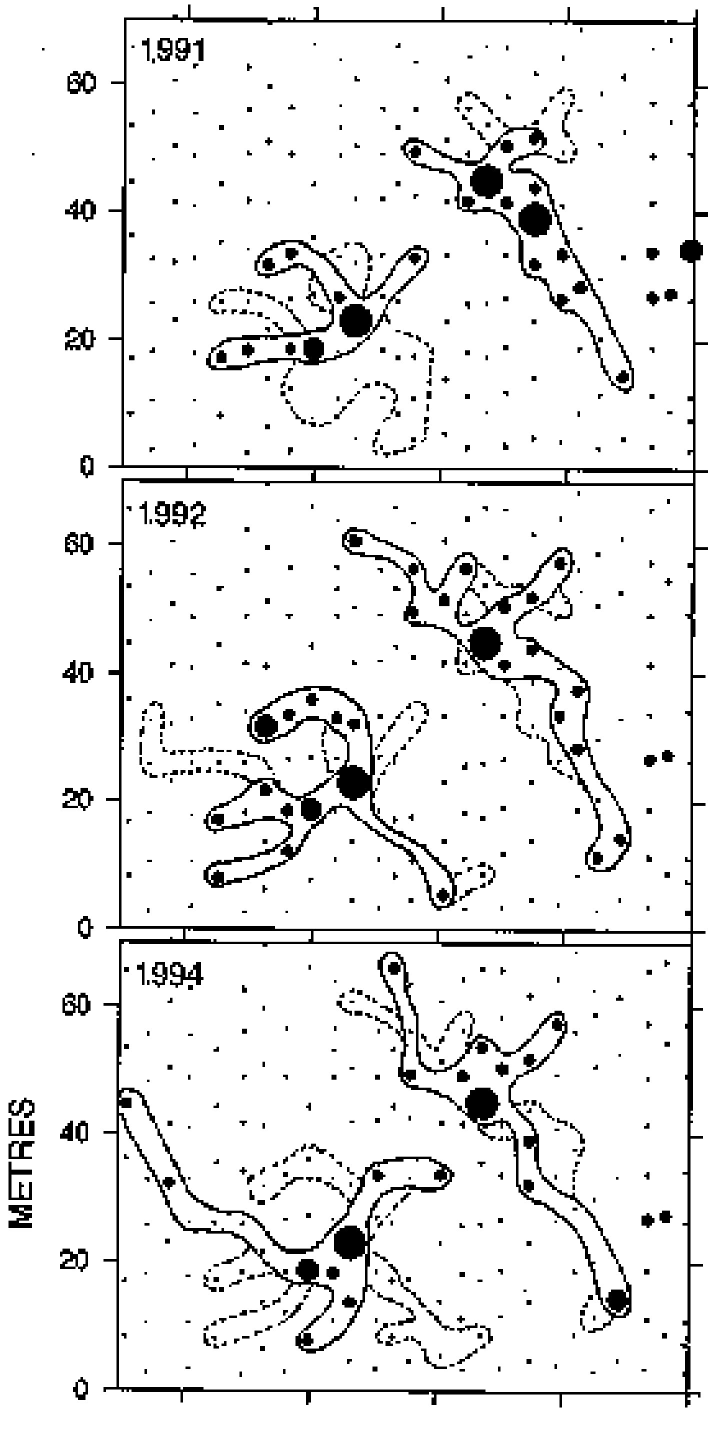


Figure 47: Dynamique du réseau de galeries de deux colonies de *N. princeps* déterminée à partir de la cartographie des nids (représentés par des grands cercles) et galeries (petits cercles) arboricoles en avril-mai 1991, 1992 et 1994. Les arbres sont représentés par des points. Les traits continus englobent le territoire présumé au moment de la cartographie et les traits pointillés les arbres portant des traces d'occupation ayant eu lieu entre deux cartographies. Les colonies d'autres espèces n'ont pas été représentées.

Annexe 7: action de la sécrétion défensive des soldats de *N. novarumhebridarum*

Méthode

La méthode adoptée est celle mise au point par Roisin *et al.* (1990). Le dispositif expérimental est schématisé à la Fig. 48. On y introduit 40 termites (40 soldats, 40 ouvriers âgés, 20 soldats et 20 ouvriers âgés). On laisse les termites s'accommoder au dispositif pendant quelques heures après lesquelles on les retrouve généralement tous regroupés sur le bout de nid. A ce moment, la sécrétion défensive est récoltée en pressant la tête de trois soldats (de même société que ceux dans la boîte de Petri) sur un carré de papier filtre de 4 mm^2 recouvert ensuite par un autre papier de même dimension pour éviter que les termites ne s'y engluent. Les papiers imprégnés de sécrétion sont aussitôt introduits dans le dispositif par un orifice foré dans le couvercle de la boîte de Petri et obturé ensuite. Les termites s'introduisant dans le cercle de Ø 33 mm sont identifiés (soldat/ouvrier) et dénombrés toutes les 30 secondes pendant 4 minutes 30 secondes. L'observation des comportements et les dénombrages sont facilités par un enregistrement vidéo de l'expérience. Des individus provenant de trois colonies ont été utilisés pour les tests. Quinze répétitions (5 par société) par type de test ont été réalisées. Des expériences témoin ont aussi été réalisées en présentant aux termites un petit carré de papier filtre vierge.

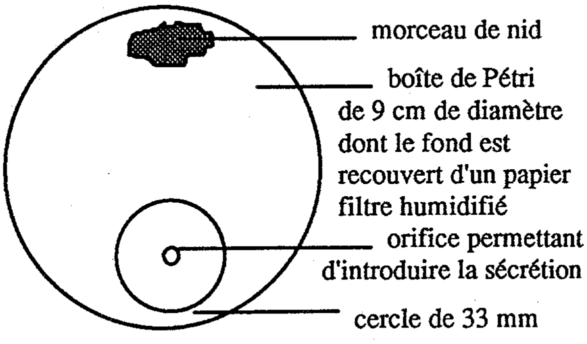


Figure 48: Dispositif expérimental utilisé pour étudier l'action phéromonale des sécrétions défensives.

Résultats

Aucune réaction n'a été provoquée par l'introduction d'un carré de papier filtre vierge. Les réactions à l'introduction de sécrétion défensive sont représentées à la Fig. 50. D'une manière générale, la sécrétion défensive a provoqué une réponse, mais très faible. Un nombre très restreint d'individus se sont approchés de la source pour reculer vivement lorsqu' ils n'en étaient plus qu'à quelques millimètres. Aucun comportement d'alarme n'a été observé après l'approche de la source.

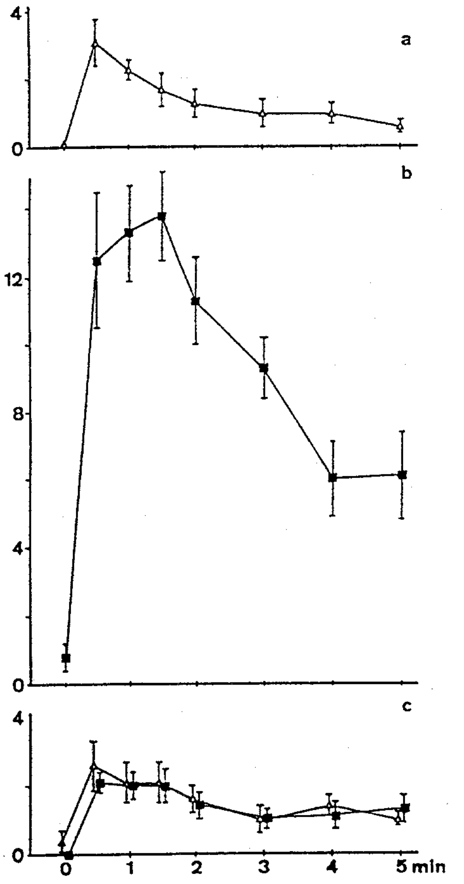


Figure 49: Réaction des soldats (▲) et des grands ouvriers âgés (■) de *N. princeps* vis-à-vis de la sécrétion défensive de leurs soldats exprimée par le nombre d'individus autour de la source (dans le cercle de 33mm) en fonction du temps. Le symbole indique la valeur moyenne et les barres l'erreur standard (n= 10 répétitions). (a) Groupe de 40 soldats (b) Groupe de 40 ouvriers (c) Groupe mixte comprenant 20 soldats et 20 ouvriers. (d'après Roisin *et al.* 1990).

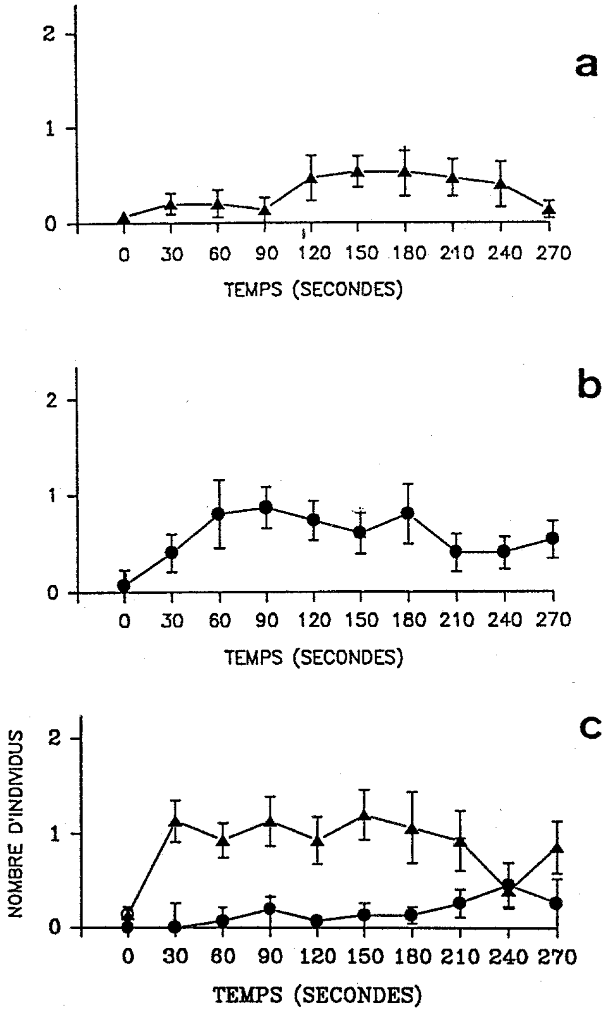


Figure 50: Réaction des soldats (▲) et des grands ouvriers âgés (●) de *N. novarumhebridarum* vis-à-vis de la sécrétion défensive de leurs soldats exprimée par le nombre d'individus autour de la source (dans le cercle de 33mm) en fonction du temps. Le symbole indique la valeur moyenne et les barres l'erreur standard (n= 15 répétitions). (a) Groupe de 40 soldats (b) Groupe de 40 ouvriers (c) Groupe mixte comprenant 20 soldats et 20 ouvriers.

Discussion

Contrairement à *N. princeps* (Fig. 49), chez *N. novarumhebridarum* la sécrétion défensive ne provoque que de très faibles réactions. Les soldats en groupes homogènes ne bougent quasiment pas de leur bout de nid (Fig. 50a) alors qu'ils sont plus actifs en groupe mixte (Fig. 50c). Inversement la réponse des ouvriers est légèrement plus forte en groupe homogène (Fig. 50b) qu'en groupe mixte (Fig. 50c). Les mêmes constations peuvent se faire, de manière nettement plus tranchée, chez *N. princeps*. Ceci suggère qu'en groupe mixte, ce qui correspond à une situation réelle, les soldats sont les plus actifs vis-à-vis d'une perturbation et que les ouvriers ne réagissent que lorsque les soldats ont été mobilisés (Roisin *et al.* 1990). Ceci souligne le rôle complémentaire des ouvriers et des soldats dans la défense et est appuyé par des observations de terrain. Dans les pistes à ciel ouvert le couloir central parcouru par les ouvriers est bordé de soldats pointant vers l'extérieur et lorsqu'on perturbe un nid ou des galeries ce sont les soldats qui affluent en première ligne.

Annexe 8: Interactions entre *M. biroi* et *N. polygynus*

N. polygynus construit préférentiellement ses nids entre les fourches des branches d'arbustes et est rare en cocoteraie. Bien que nous n'ayons pas pu observer le déroulement de l'attaque de nids de *M. biroi* par *N. polygynus*, une série d'observations porte à croire que *N. polygynus*, à l'instar de *N. princeps* et *N. novarumhebridarum*, interagit de manière agressive avec *M. biroi*. Une parcelle de 1.1 ha, envahie par des *N. polygynus* a été cartographiée en Juillet 1993. A l'origine, ce site était une plantation pure de cocotiers qui a été interplantée de cacaoyers vers 1978. En juillet 1993 *N. polygynus* occupait 82% (116/142) des cocotiers présents et 46% (56/123) des cacaoyers. Parmi les arbres occupés par des *N. polygynus,* 86% (100/116) des cocotiers et 30% (17/56) des cacaoyers ont été trouvés avec des traces d'occupation antérieure par *M. biroi* (vestiges de nids ou de galeries). Seul 3 nids de *M. biroi* étaient encore vivants. D'autres nids de *M. biroi* avaient été, selon toute vraisemblance, récemment envahis puisque des cadavres de *M. biroi* et de *N. polygynus* se côtoyaient à la fois à l'intérieur et à l'extérieur du nid. Des galeries de *N. polygynus* entouraient le pourtour des nids de *M. biroi* envahis exactement de la même façon qu'observée chez *N. princeps* (voir Fig 14 p. 32). Il est probable que l'introduction de cacaoyers dans la parcelle a procuré un support favorable pour les nids de *N. polygynus* et a permis l'invasion de la parcelle aux dépens des colonies de *M. biroi* initialement présentes. Les nids de *M. biroi* récemment envahis ont été disséqués et les *N. polygynus*, plus petits que les *N. princeps* et les *N. novarumhebridarum*, ont été observés circulant sans difficulté à travers les orifices étroits séparant les chambres du nid de *M. biroi*. Lors de l'attaque d'un nid de *M. biroi*, il est probable que les *N. polygynus* bénéficient d'un avantage numérique grâce à l'organisation hautement polycalique de leurs colonies.

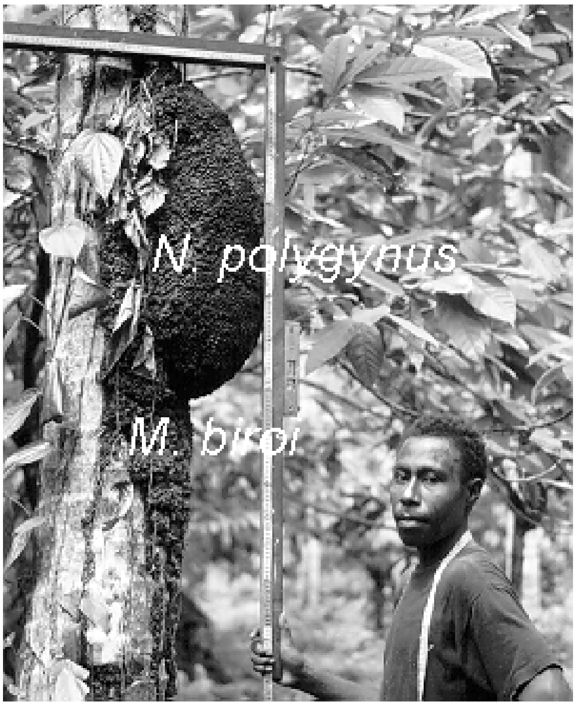


Figure 51: nid de *N. polygynus* construit sur un nid de *M. biroi*

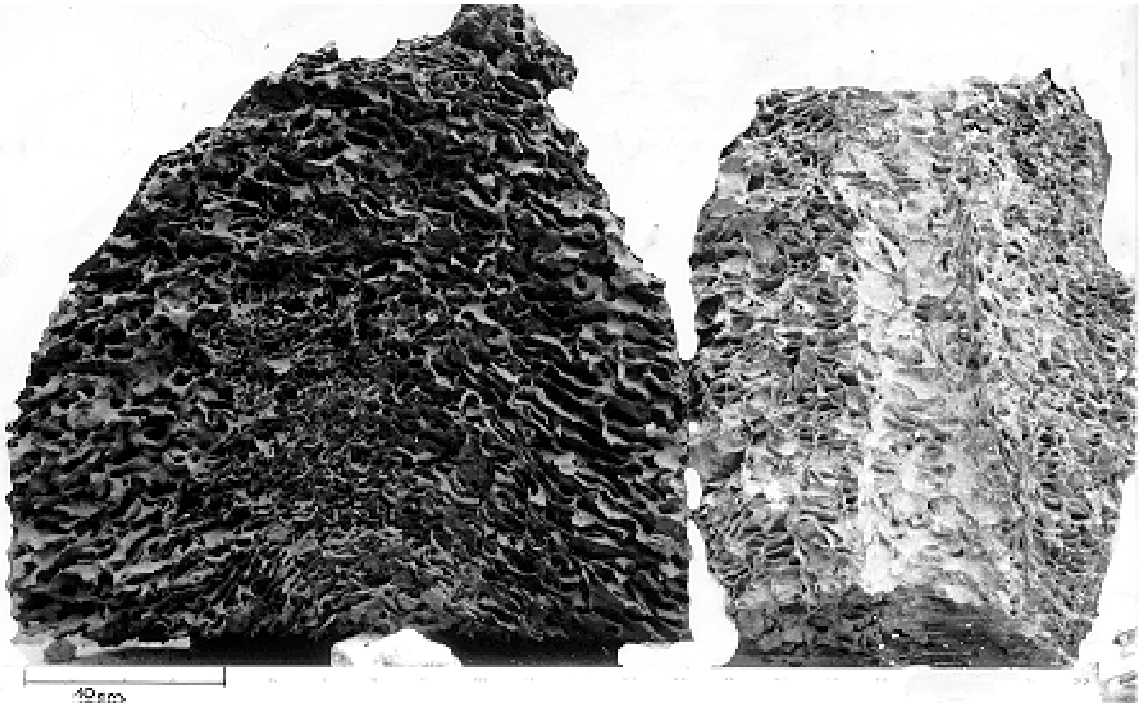
Annexe 9: Architecture des nids

Les trois espèces peuvent se distinguer par l'architecture de leurs nids. De par leur géométrie tout d'abord: les nids de *M. biroi* ont une forme qui s'apparente à un secteur de cylindre creux tandis que celle des *Nasutitermes* s'approche d'un ellipsoïde de révolution dont le centre se situe sur l'écorce du cocotier. Le volume des nids peut aussi être un caractère distinctif surtout entre les *Nasutitermes* dont les nids ont la même forme. Les nids de *N. novarumhebridarum* ont en moyenne une vingtaine de dm^3 et ne dépassent jamais 85 dm^3 tandis que les nids de *N. princeps* ont un volume moyen d'une cinquantaine de dm^3 et peuvent atteindre plus de 300 dm^3. Les nids de *M. biroi* ont en moyenne une dizaine de dm^3 et atteignent exceptionnellement près de 80 dm^3.

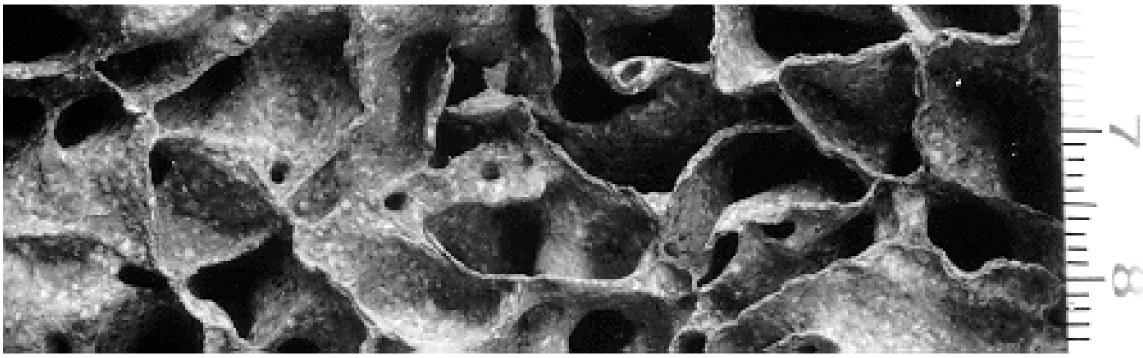
La texture des nids n'est pas la même chez *M. biroi* et les deux *Nasutitermes* spp. La surface extérieure des nids de *M. biroi* est composée d'une multitude de petites stalactites. Les nids de *Nasutitermes* ont une surface extérieure faite de légères ondulations typiques des *Nasutitermes* arboricoles (Grassé 1986). Si la surface extérieure des *Nasutitermes* consiste en une fragile pellicule qui s'enlève comme une peau d'orange, par contre chez *M. biroi* elle fait bloc avec le reste du nid. La cellule royale est toujours l'endroit le plus renforcé du nid. En son centre, se trouve une large chambre horizontale abritant le couple royal. Elle peut aussi être composée d'une série de chambres superposées dans les nids contenant des sexués secondaires.

L'architecture interne des nids est fort différente entre *Nasutitermes* et *M. biroi* (Fig. 52 A). Les nids de *M.biroi* sont composés de chambres communiquant par de petits orifices (Fig. 52B) ne permettant le passage que d'un termite à la fois et correspondant précisement aux dimensions de la capsule céphalique des soldats qui sont ainsi capables de les obturer (Deligne & Pasteels 1982) (Fig. 52C). Tout au contraire, les chambres de *Nasutitermes* sont ouvertes permettant une bonne diffusion des signaux chimiques et de rapides mouvements de troupes. Une coupe dans ces nids révèle, comme chez d'autres *Nasutitermes* (e.g. *N. corniger* Thorne 1980), l'existence d'une zone périphérique à grandes cellules et d'une zone corticale plus dense.

Figure 52 (page suivante)**:** Comparaison de l'architecture des nids de *M. biroi* et de *N. princeps*. A: coupe dans un nid de *N. princeps* (à gauche) permettant de voir les régions corticales et périphériques du nid et coupe dans un nid de *M. biroi* aux chambres beaucoup plus fermées (distance entre 2 grands traits = 10cm). B: Gros plan du nid de *M. biroi* permettant de distinguer les orifices de communication entre chambres (distance entre 2 grands traits = 10mm). C: Soldat de *M. biroi* obturant un orifice au moyen de sa capsule céphalique.



▲A ▼B



▼ C

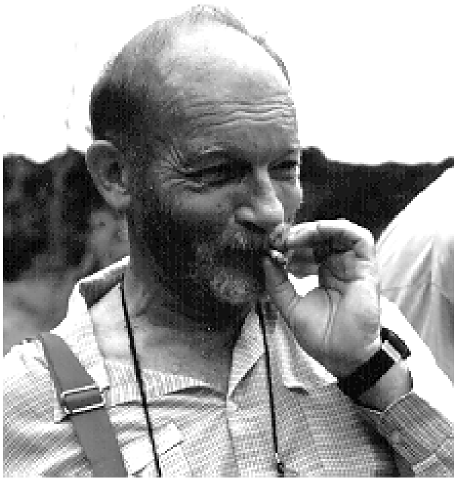
Remerciements

Mes plus chaleureux remerciements vont au Prof. **Jacques Pasteels** (à droite), directeur du laboratoire de biologie des communautés animales, (accompagné sur la photo par **Anton**, chef du village d'Awar). Jacques Pasteels force l'admiration de par sa culture et de par ses qualités tant professionnelles qu'humaines. Il a su remarquablement me guider durant mes recherches, toujours disponible malgré la multitude de ses activités. Travailler dans son laboratoire est un privillège.

Le Dr. **Yves Roisin,** saisi ici dans son attitude typique devant une nouvelle termitière, a très étroitement participé à ce travail. Il m'a fait bénéficier de l'expérience acquise au cours de sa propre thèse, m'a orienté vers des voies prometteuses et, lors de la rédaction a grandement contribué à la clarification, à l'allègement du texte et au développement de certaines idées. La profondeur de ses connaissances n'a d'égal que son humour subtil.

Lu à l'envers "LAING" devient "GNIAL", comme l'idée d'y avoir créé une station de recherche due aux Professeurs Bouillon et Tursch.

Le Professeur **Jean Bouillon** (à droite), co-directeur de la Station (accompagné sur la photo de **Miller Magap,** le technicien de la Station) m'y a accueilli avec beaucoup de bienveillance et j'ai pu y poursuivre mes recherches dans de très bonnes conditions. L'île de Laing, qu'il qualifie avec humour "d'enfer de l'homme blanc", m'a rapidement conquis et j'y ai passé des moments inoubliables.



Le Professeur **Ben Tursch** (photo ci-contre) est à l'origine de beaucoup de ceux-ci, apportant beaucoup de bonne humeur. Sa cigarette continuellement allumée nous a efficacement prémuni des moustiques. Je remercie Ben Tursch pour son aide et ses conseils notamment pour le traitement des images. Le Dr **Claude Everaerts** a été d'une grande contribution en me fournissant de nombreuses références bibliographiques et de par d'intéressantes suggestions lors des expériences sur l'agressivité intra-spécifique. Le Prof. **Jean Deligne** et le Prof. **Guy Josens** m'ont fait bénéficier de leur connaissance approfondie des termites. Je remercie pour leurs conseils et suggestions le Dr. **Patrick Grootaert**, le Dr. **Georges Wauthy** et le Prof. **Philippe Lebrun**. Je remercie pour l'identification des plantes le Prof. **Vincent Demoulin**, Ulg, pour l'identification des algues le Dr. **Lucien Hoffmann**, Ulg; pour l'identification des bryophytes le Dr. **Timo Koponen**; pour l'identification des fourmis le Dr. **Roger Cammaerts**, ULB, le Dr. **Robert Taylor** CSIRO et le Dr. **Claire Detrain**, ULB. Pour son aide dans certains traitements mathématiques je remercie le Dr. **Jacqueline Sengier.** Pour ses conseils et suggestions quant aux traitements statistiques et traitements graphiques ainsi que pour sa chaleureuse amitié, je remercie le Dr. **Marc Roche**, Ulg.

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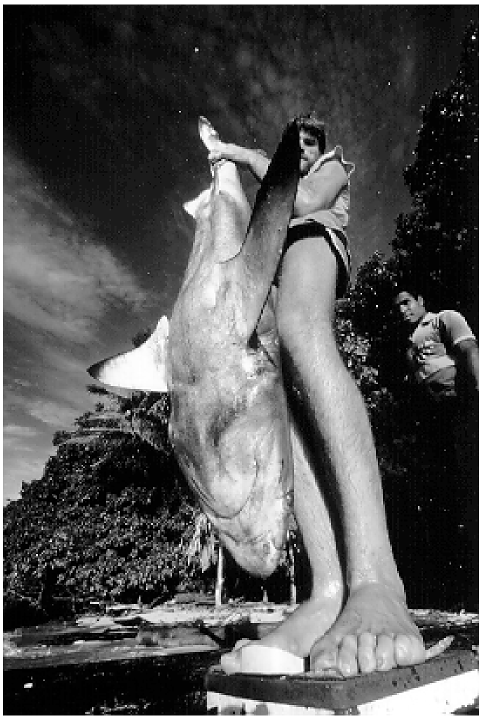

John et **Susan Beck** m'ont accueilli avec chaleur et hospitalité à Madang. Le chien **Nando** (ci-contre) m'a été d'un grand réconfort moral lors des moments de solitude à l'île .

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Cette thèse est dédiée à **Natalie** ...