

Environmental Influences on the Arboreal Nesting Termite Community in New Guinean Coconut Plantations

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ABSTRACT Three species of arboreal nesting termites common in New Guinean coconut plantations: *Microcerotermes biroi* (Desneux), *Nasutitermes princeps* (Desneux), and *Nasutitermes novarumhebridarum* (N. and K. Holmgren), are in competition with each other. This work evaluated the influence of environmental factors on this community. We compared the arboreal nesting termite distribution, abundance, and colony size in the following 3 types of coconut plantation: (1) open plantations with tall trees (≈ 25 m) at low density (≤ 100 trees per hectare); (2) standard plantations with medium size trees (≈ 13 m) at standard density (100–180 trees per hectare); (3) dense plantations (180–300 trees per hectare) 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. novarumhebridarum* occupied $\approx 2\%$ 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

THREE COMMON ARBOREAL nesting termites in New Guinean coconut plantations, *Microcerotermes biroi* (Desneux), *Nasutitermes princeps* (Desneux), and *Nasutitermes novarumhebridarum* (N. and K. Holmgren), occupy exclusive territories forming a mosaic reminiscent of those observed in ants. They use identical nesting sites—coconut tree trunk—and have similar food habits, consuming dead cellulosic material on the coconut tree or on the ground (for example, palm leaves, inflorescences). The 3 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*. Like *M. biroi*, *N. novarumhebridarum* relies on alates to colonize new sites, but seems preferentially associated with dead coconut trees (Roisin and Pasteels 1987).

In addition to 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 and Levings (1987) demonstrated that the mosaic of territories of *Nasutitermes nigriceps* (Haldeman) and *N. corniger* (Motschulsky) was affected by the identity of the dominant mangrove tree. In *Rhizophora mangale* Linnaeus 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 char-

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acteristics 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* (Latreille) and *Tetramorium* (formerly *Macromischoides*) *aculeatum* (Mayr) (Majer 1976).

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 2 *Nasutitermes* species (Roisin and Pasteels 1985, 1986, 1987) and presented evidence for territoriality and competition with *M. biroi*. 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 3 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 <100 trees per hectare and sunlight is high in this habitat.

Standard Plantations. Plantations of medium size trees (≈ 13 m) at a density between 100 and 180 trees per hectare; trees are generally 8–9 m distant from each other and planted according to a square or triangular pattern (Department of Primary Industry 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 es-

tablished by German planters; as a result, the tree height may range from 13 to 25 m and trees of various height are often mixed. Density is between 180 and 300 trees per hectare. This habitat is well shaded.

Coconut trees used in plantations were tall varieties and did not change until the late 1970s when hybrid and dwarf varieties were introduced. Our observations were conducted only in plantations with ages of >30 yr. Our plantation typology was consistent with differences in ground vegetation. In open plantations the grasses *Pennisetum macrostachyum* (Brongniart) Trinius, *Imperata cylindrica* (L.) Palisot de Beauvois, *Chloris barbata* Swartz 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 and 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).

Twenty-nine quadrats were mapped between September 1990 and April 1994 (Table 1). 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 5°. Tree condition (for example, healthy, burnt, stump) was also noted.

Plots I–XV were selected randomly 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 1st series, because they did not match all the standardized conditions, or plots selected nonrandomly 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 yr 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 in-

Table 1. Characteristics of plots where termites were sampled

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

tercropped 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*. Nest volume was used as an indicator of nest population size because a good correlation was found between these 2 factors in the arboreal neotropical species *N. corniger* and *N. ephratae* (Holmgren) (Thorne 1985). Finding 2 (or even 3 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 1 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 (Lambrech KG, Göttingen, type 252 Ua or Jules Richard, Paris, 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 2 thermohygrographs fitted with a temperature/humidity probe (Hanna HI 8564 and Acez, Singapore) and in 1994 with a Solomat MPM4000 (Solomat, Bristol, UK) environment recorder equipped with 2 thermometer probes (Pt 100 and thermocouple). One of the probes was inserted in a PVC pipe (2.54 cm diameter) 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 and Noirot 1958), the PVC pipe was inserted into the nest at least 1 wk 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 2nd probe was put in a meteorological cabinet to measure the external air temperature. Temperature recordings started 24 h after installing the probes. Four nests of *M. biroi* and 4 nests of *N. princeps* were studied. One nest of *M. biroi* was killed with ethyl acetate and Baygon (Bayer) 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 and Orientation of Raintracks. Tree inclination was measured with a plumb line and a protractor. The direction in which trees were leaning was measured with a compass. The extent and orientation of raintracks (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 1-way ANOVA on transformed data: $F = 14.082$; $df = 2, 12$; $P <$

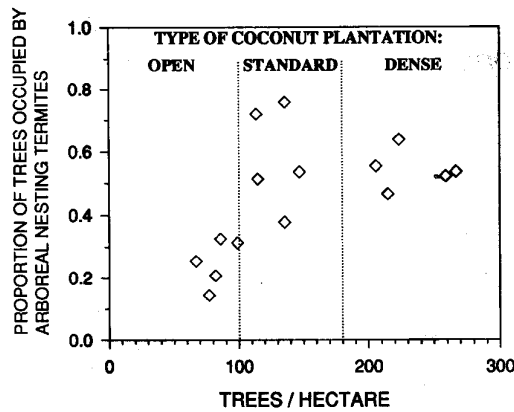


Fig. 1. Proportion of trees occupied by arboreal nesting termites in plots I–XV corresponding to the 3 plantation types.

0.001) (Fig. 1). 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, $P = 0.811$).

The proportion of coconut trees occupied by nests or galleries of *M. biroi* differed among plantation types (1-way ANOVA, $F = 20.269$; $df = 2, 12$; $P = 0.001$) (Fig. 2). *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* (1-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* ($m = 2%$, 1-way ANOVA, $F = 1.420$; $df = 2, 12$; $P = 0.280$).

Nest Volumes. Nest volumes of *M. biroi* (Fig. 3) varied significantly among plantation types (plots I–XV, 1-way ANOVA, $F = 7.762$; $df = 2, 740$; $P < 0.01$). Average nest volume per tree in open plantations (mean \pm SD, 9.1 ± 6.7 liters, $n = 49$) was not significantly different from that observed in standard plantations ($m = 10.8 \pm 9.2$ liters, $n = 267$) (Tukey, $P = 0.577$) but was smaller than in dense plantations ($m = 13.5 \pm 11.6$ liters, $n = 427$; Tukey, $P < 0.05$).

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

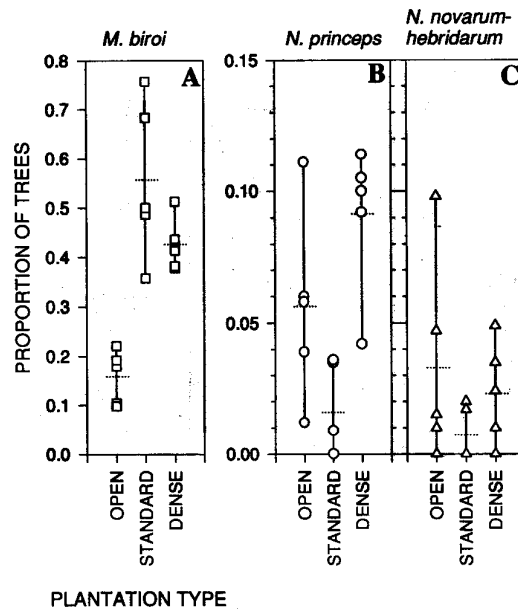


Fig. 2. Proportion of trees occupied by (A) *M. biroi*, (B) *N. princeps*, and (C) *N. novarumhebridarum* in the 3 plantation types. Hollow symbols represent observed values, dotted lines represent averages.

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; 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, 1-way ANOVA, $F = 7.839$; $df = 2, 62$; $P < 0.01$). Average nest volume in dense plantations ($m = 80.2 \pm 67.7$ liters, $n = 39$) was significantly larger than in open ($m = 23.2 \pm 25.2$ liters, $n = 16$, Tukey, $P < 0.01$) or standard plantations ($m = 25.9 \pm 32.9$ 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 ANOVA of *N. novarumhebridarum* nest volumes among the 3 plantation types led to the same conclusions as for *N. princeps* (plots I–XXV, 1-way ANOVA, $F = 5.547$; $df = 2, 43$; $P < 0.01$): average nest volumes did not differ between open plantations ($m = 12.1 \pm 14.1$ liters, $n = 10$) and standard ones ($m = 8.8 \pm 6.9$ liters, $n = 8$, Tukey, $P = 0.934$), but were significantly larger in dense plantations ($m = 30.7 \pm 23.7$ liters, $n = 28$; Tukey, $P < 0.05$).

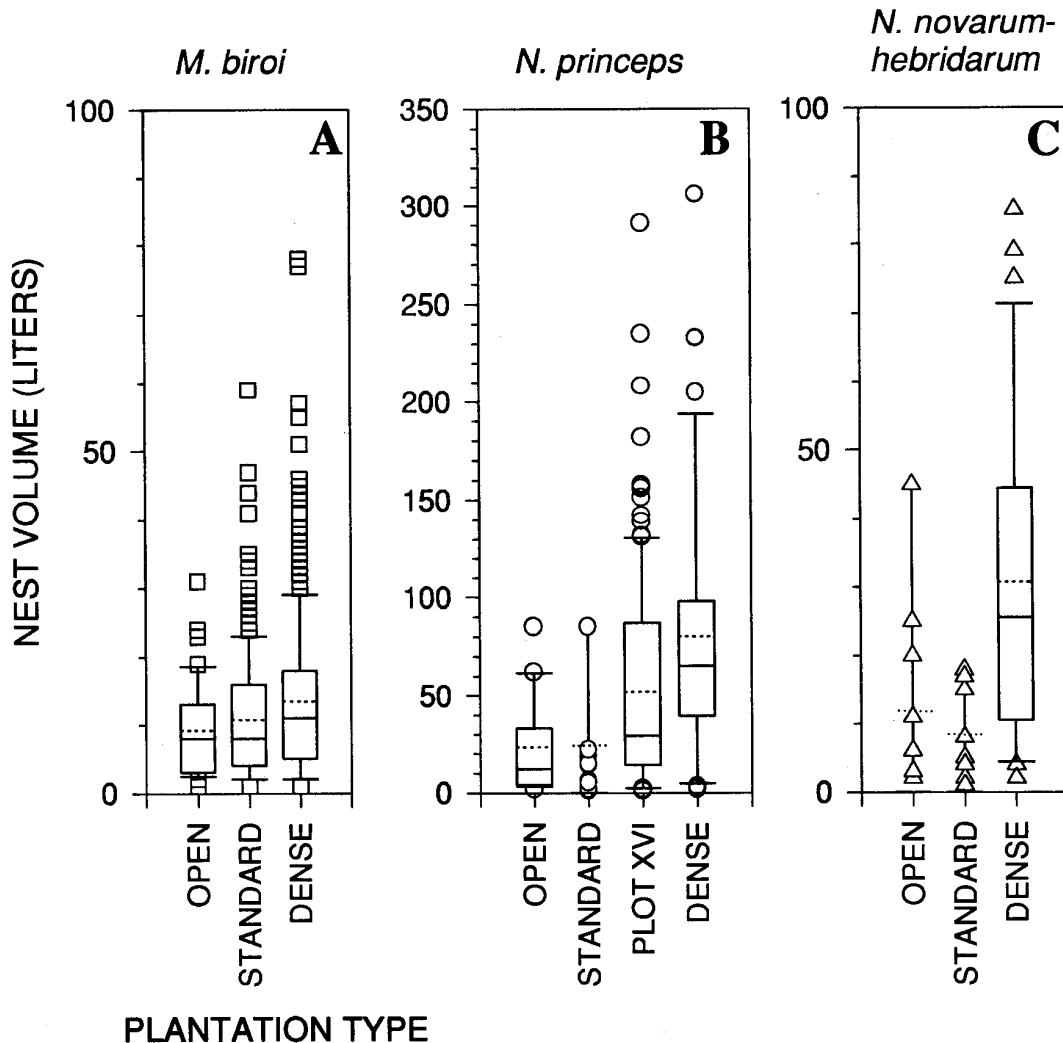


Fig. 3. Distribution of nests volumes for *M. biroi* (A, data from plots I–XV), *N. princeps* (B, plots I–XV and XVII–XXV, presumed unicolonial nests of plot XVI) and *N. novarumhebridarum* (C, plots I–XXV) in the 3 plantation types. Box plots were used when >15 values were available, otherwise all observed 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 individual symbols.

Territory Area. Colonies of *M. biroi* generally occupied 1–3 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 ($m = 31.7$ m) from the nest. In open or standard plantations (plots I–X), a col-

ony occupied 2–4 trees ($m = 2.6$), the most remote of which was situated 5–39 m ($m = 14.8$ m) 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 0.7 m in 25% of the nests, below

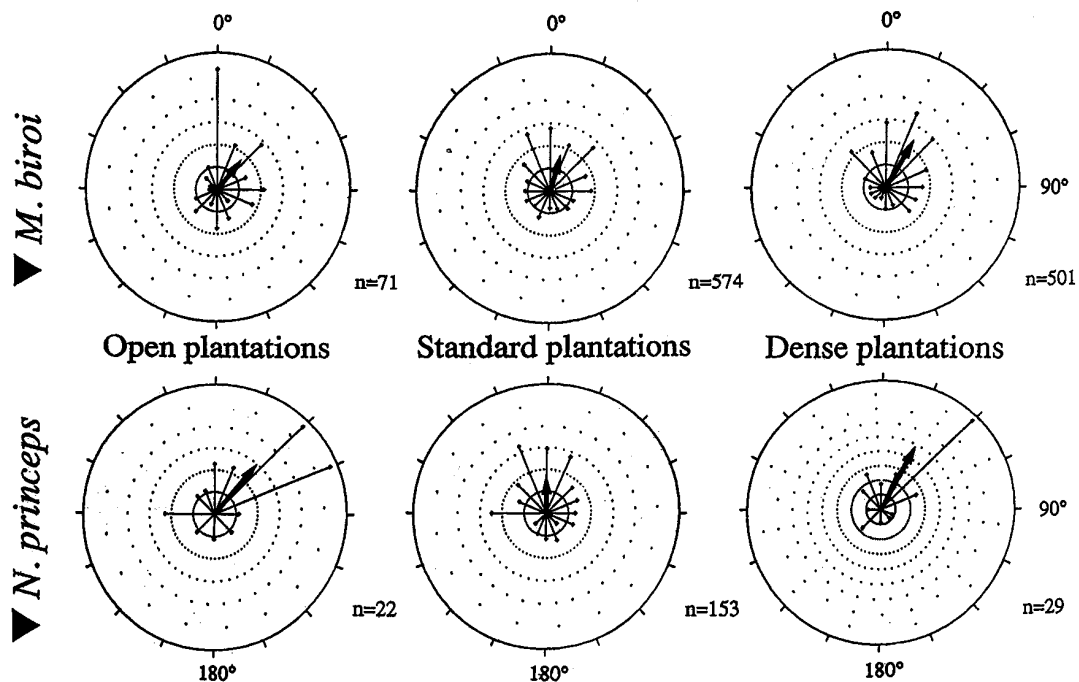


Fig. 4. Circular histograms for orientation of *M. biroi* nests and *N. princeps* nests in the 3 plantation types. For example, magnetic north = 0°, east = 90°. True north lies $\approx 6^\circ$ east of magnetic north. Each concentric circle represents a frequency increment of 4%. Arrows represent the mean vector which may range from 0 (no mean direction) to 1 (all nests concentrated at the same direction).

1.1 m in 50%, below 2.0 m in 75%, and below 4.5 m in 90% ($n = 1,140$). 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 northeast (Fig. 4), but mean angles were significantly different among plantation types (plots I–XXV, Watson–Williams test for circular distributions: $F = 3.571$; $df = 2, 1,143$; $P < 0.05$): $41 \pm 92^\circ$ (mean angle \pm circular standard deviation, mean vector length $\rho_1 = 0.28$) in open plantations ($n = 71$); $16 \pm 94^\circ$ in standard plantations ($n = 574$, $\rho_1 = 0.26$); $29 \pm 81^\circ$ in dense plantations ($n = 501$, $\rho_1 = 0.37$). Although the sample size was much smaller, nests of *N. princeps* also showed a prevailing north–east orientation (Fig. 4), with mean angles significantly different among plantation types (Watson–Williams test, $F = 3.427$, $df = 2, 204$; $P < 0.05$): $41 \pm 64^\circ$ in open plantations ($n = 22$, $\rho_1 = 0.51$); $0 \pm 90^\circ$ in standard plantations ($n = 153$, $\rho_1 = 0.29$); $28 \pm 64^\circ$ in dense plantations ($n = 29$, $\rho_1 = 0.54$). Regarding *N. no-*

varumhebridarum, too few data were available to perform a statistical analysis on nest orientation.

Effect of Environmental Variables on Termites. Temperature and Humidity. Air temperature and humidity in the shade were measured in the 3 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 2 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 <70%. At night and during rains, relative humidity reached saturation.

Figure 5 shows temperature variations under the surface and in the core of a nest of *M. biroi* (Fig. 5A) and a nest of *N. princeps* (Fig. 5B) in comparable conditions: both nests had the same northeast orientation and were surveyed in open plot I in April 1994. The surface temperature of both nests increased abruptly from 0700 hours, because they were exposed to direct sunlight, to reach a maximum around 1000 hours. The surface temperature then slowly decreased. Temperature

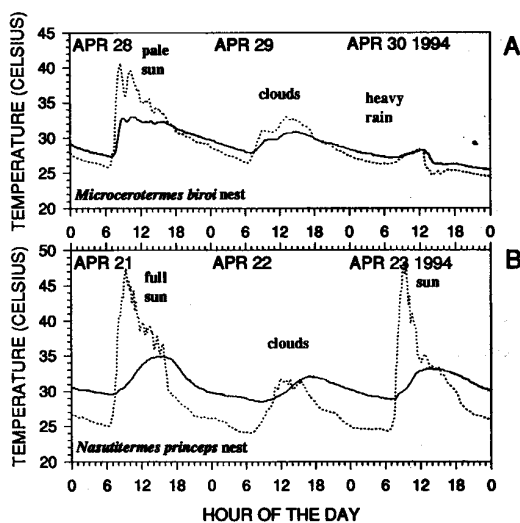


Fig. 5. Temperature variation recorded every 10 min at the center (solid line) and under the surface (dotted line) of northeasterly oriented nests of *M. biroi* (A), orientation 50°, and *N. princeps* (B), orientation 55°.

records of other nests showed that surface temperature can reach 50°C in both species. Figure 5 also reveals that the relationship between nest surface and core temperature is markedly different between the 2 species. In *M. biroi*, core temperature followed almost exactly ups and downs of surface temperature, though with a lower amplitude. In *N. princeps*, core temperature varied in a much delayed and smoothed 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, 12–14 May 1993, was 27.5–31.1°C, with an external air temperature of 24.2–29.6°C; dead nest temperature, 22–24 June 1993, ranged between 27.2 and 29.3°C, with an external air temperature of 25.2–32.2°C. Relative humidity in the core of 2 *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 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 $\chi^2 = 2.029$, $df = 1$, $P > 0.05$), but not by the same termite species ($\chi^2 = 61.597$, $df = 2$, $P < 0.001$); the occurrence of *N. novarumhebridarum* was almost 4 times as frequent on dead trees as on live ones (12.7 versus 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 2).

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 $94 \pm 60^\circ$ of the circumference ($n = 93$; range, 10–282°, orienta-

Table 2. 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	<i>M. biroi</i>	<i>N. princeps</i>	<i>N. novarumhebridarum</i>	No termites	Total
Alive	1,617 (946 n + 671 g)	527 (158 n + 369 g)	156 (71 n + 85 g)	2,531	4,831
Dead	52 (17 n + 35 g)	39 (10 n + 29 g)	29 (8 n + 21 g)	108	228
Total	1,669	566	185	2,639	5,059
% on dead trees	3.1%	6.9%	15.7%	4.1%	4.5%

tion: $6 \pm 65^\circ$, mean vector length $\rho_1 = 0.53$). Presence of *M. biroi* nests was independent from the presence of a raintrack in plots XIV and XXIV (Cochran corrected $\chi^2 = 0.194$, $df = 1$, $P > 0.05$) 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 2 *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 2 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 $\approx 8^\circ$.

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 2 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* (Wasmann) rose and fell with

the outside temperature. The tolerance of *M. biroi* to high temperatures is not known, but temperatures of 40–50°C under the nest surface are high for a termite. Mitchell et al. (1993) demonstrated that the critical thermal maximum of *Hodotermes mossambicus* (Hagen), a termite living in arid areas, ranged between 43.5 and 48.5°C. Collins et al. (1973) established that *Gnathamitermes perplexus* (Banks), another desert-living termite, had an outstanding temperature tolerance and foraged between 9 and 49°C. The temperature near the core of termite nests generally ranges between 25 and 35°C, with uppermost values of 38°C (Holdaway and Gay 1948, Lüscher 1961, Greaves 1964, Josens 1971, Malaka 1977, Watson and Abbey 1986, Bristow and Holt 1987). 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 Fig. 5 A and B 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 warm up or cool 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 (Holdaway and Gay 1948, Greaves 1964, Peakin and Josens 1978, Watson and Abbey 1986), 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 desiccated by sunlight. By contrast, as tree density increases, food items on the ground are better protected from desiccation 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 connections 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 and Pasteels 1985, 1986; 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 1985), 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 and Pasteels 1987). 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 2 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. 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 3 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 and Calaby 1970, Grigg 1973, Grigg and Underwood 1977, Jacklyn 1991), *Drepanotermes perniger* (Froggatt) (Watson and Perry 1981), *Tumulitermes hastilis* (Froggatt) (Hill 1942), and ants (*Solenopsis invicta* (Buren), Hubbard and Cunningham 1977) and is interpreted as favoring thermoregulation. For example, north-south orientation of wedge-shaped mounds of *Amitermes laurensis* (Mjöberg) 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 *A. laurensis* (calculated from the data of Grigg and Underwood 1977). Finally, a significant difference in mean nest orientation was also observed between the 3 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 rain-tracks. 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 and Pasteels 1987). 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 and Pasteels 1987).

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