Environmental Factors Related to the Occurrence of Mound-Building Nasute Termites in Trachypogon Savannas of the Orinoco Llanos[1]

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ABSTRACT

The incidence of termite mounds was determined in twenty-six sites in the Trachypogon savannas at the Orinoco Llanos, including a wide range of physionomic types. A multiple discriminate analysis was utilized to analyze ecological variables as the best indicators of a given area's suitability for support of terrestrial *Velocitermes* and/or *Nasutitermes* species. The variables included physical attributes (texture, ineffective soil mass, water holding capacity, and infiltration rate), chemical attributes (cation exchange capacity, base saturation, and organic matter content), soil characteristics, and the above-ground phytomass accumulated at each stand. Results indicated that soil physical variables determining water balance during critical dry periods were of paramount value for the successful establishment of mound-building nasute termites in Trachypogon savannas.

RESUMEN

Se determinó la incidencia de nidos de termitas en veintiseis rodales, correspondientes a la gama de tipos fisonómicos de sabanas de Trachypogon que se encuentran en Los Llanos del Orinoco. Variables ecológicas, como indicadores de la capacidad del área para mantener a especies terrestres de *Velocitermes* sp. y/o *Nasutitermes* spp., fueron estudiadas mediante un análisis múltiple discriminante. Los atributos medidos se relacionaron con características físicas (textura, volumen ineficaz de suelo capacidad de retención de humedad, y tasa de infiltración) y químicas del suelo (capacidad de intercambio catiónico, saturación con bases, contenido de materia orgánica), y la cantidad de fitomasa epígea acumulada en cada rodal. Los resultados parecen indicar que variables relacionadas con las características edáficas, que inciden sobre el balance hídrico durante los períodos críticos de sequía, fueron de importancia crucial en determinar la presencia de nasute-termitas en las sabanas de Trachypogon.

EARTHEN MOUNDS OF THE TERMITES *Nasutitermes* spp. are conspicuous features of many Trachypogon savannas of the Orinoco Llanos (Beard 1953; Goodland 1965, 1966; Galvis *et al.* 1978), especially when the mounds are exposed by vegetation fires during the dry season. The pattern of termite mounds in each of the different physionomic types of savanna is far from uniform; the savannas may be densely populated or have no mounds at all. We investigated underlying causes of the small and medium scale patterns.

Distribution patterns of termite mounds have been studied previously in both savannas and dry woodlands. On a relatively small-scale study, Nel and Malan (1974) fit the mound abundance of *Trinervitermis trinervoides* (Sjosted) in the South African veld to negative binomial distribution. For the Trachypogon savannas of the Eastern Colombian Llanos the distribution of *Coptotermes* and *Nasutitermes* mounds were significantly contagious (Galvis *et al.* 1978). In two grassland formations in Central Brazil, Lacher *et al.* (1986) found changes in density and termite community composition between two sites with differences in the humidity regime at the same campo limpo. Holt *et al.* (1980) studied the occurrence of six species of termite on "red" and "yellow" soils supporting dry woodland in northeastern Australia. They found statistically significant species differences in the mound distribution pattern and interpreted these as preferences for soil types which differed largely in physical characteristics related to the water regime. Relations between the density of *Macrotermes* mounds and the rainfall, minimum temperature, and exchangeable bases were established in Uganda by Pomeroy (1978) by a multivariate analysis of environmental factors.

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FIGURE 1. Locations of Trachypogon savannas at the Orinoco Llanos (Venezuela). The scale = 1:4,000,000.

We analyzed the ecological factors affecting the occurrence of termite mounds within and among physionomic types of Trachypogon savannas from the central and eastern Orinoco Llanos of Venezuela. These savannas exhibit relatively similar macroclimates but considerable edaphic and floristic diversity (San Jose *et al.* 1985).

MATERIALS AND METHODS

The studies of patterns within savannas were done at the Estación Biológica de Los Llanos (EBLL) located 10 km SSE of Calabozo in the State of Guárico, Venezuela (8°56'N, 67°25'W). Annual mean rainfall was 1257 mm with a 4-month dry season (December–March). The station grounds include 260 ha which have been protected from fire and cattle since 1960. Although changes toward a denser arboreal community is occurring under this regime (San Jose & Fariñas 1983), large patches of grassland still cover the area. Two sites were selected at the EBLL. On the first one, the native grasses *Trachypogon plumosus* (Humb. & Bonpl.) Nees and *Axonopus cancescens* (Trin) Pilger dominate on the highest microtopographic ground with ironstone outcrops. This habitat is hereafter referred to as "gravel texture site." Lower terrain covered with finer soils, on a deeper hardpan (>0.30 cm) has been almost taken over by *Hyparrhenia rufa* (Ness) Stapf, a coarse African grass introduced during the early 1950's. This habitat was termed "fine texture site." Outside the station boundary, where the land is grazed by cattle and burned annually, trees occur in smaller, more isolated patches, and there is less *H. rufa* in the savanna; this unprotected area was refered to as "burned gravel texture site."

Censuses of termite mounds were carried out (n quadrats of 250 m^2 each) along one transect, 5 m wide and a total of 1500 m long at the gravel texture site (N = 18), the fine texture site (N = 20), and the burned gravel texture site (N = 7). Species determinations were made on the basis of microscopic examinations of inhabitants from mounds.

The study of patterns among savannas was done at 26 sites including the physionomic types of Trachypogon savannas observed at the Orinoco Llanos of Venezuela (Fig. 1), except for the Mochima site on the coastal range. The abundance of mounds was estimated by a census of 20 quadrats (250 m^2 per site), randomly chosen in each area and where soil vegetational analyses had been previously carried out.

The 26 sites were analyzed for essential primary production features and edaphic characteristics. At each site, ten 1 m^2 samples were harvested at the time of maximum aboveground phytomass in the producing season (August–September). At harvest this material was visually separated into photosynthetic (chlorophyllous material) and non-photosynthetic phytomass, and superficial litter was also collected. Samples were oven dried at 80°C to constant dry weight.

The triplicate soil samples were analyzed as follows: **pH** was measured using a glass electrode in a 2:5 soil: water slurry; percent **organic carbon** was measured by the Walkley and Black method (Jackson 1958); **exchangeable cations** were extracted with 1N NH_4Cl and their concentration was determined by atomic absorption spectrophotometry with a Varian AA-6 Spectrophotometer; **weight proportions** of the different types of particles were determined by the BOUYOUCOS methods (Day 1965); **matric potential** (water holding capacity) was measured with a pressure membrane apparatus (Richards 1949); **infiltration rate** was determined from infiltration curves as established with calibrated cylinders (Pla Sentis 1977), and **bulk density** from the volume occupied by the soil samples in field conditions (San Jose 1977).

RESULTS

The abundance of *Velocitermes paucipilus* Mathews mounds within the Biological Station (EBLL, Calabozo) did not differ significantly between the "gravel texture site" (202 ± 61 mounds ha^{-1}, N (number of quadrats) = 19) and the "fine texture site" (204 ± 42 mounds ha^{-1}, N = 20) by Mann-Whitney U-test (Sokal & Rohlf 1981). However, *Nasutitermes* spp. were found almost exclusively in "gravel texture sites" (122 ± 23 mounds ha^{-1} vs 3 ± 2 mounds ha^{-1} in "fine texture sites") and 36 ± 50 mounds ha^{-1} of exclusively *Nasutitermes* spp. were found in the "burned gravel texture site" (outside the EBLL). Comparisons among the three sample sites (Kruskal Wallis test in Sokal & Rohlf 1981) indicate that significantly fewer mounds of *Nasutitermes* spp. were observed in the fine texture and burned gravel texture sites than in the gravel texture site.

Selected variables from the sites for studying the factors affecting the occurrence of termites' mounds were classified in three different ways: (i) presence or absence of mounds of either or both genera; (Table 1); (ii) presence or absence of *Nasutitermes*; and (iii) presence or absence of *Velocitermes*. Variable mean values were calculated for each site and the mean of the means was used for a discriminant analysis (Snedecor & Cochran 1967, Hair *et al.* 1984). This multivariate technique allowed us to study the extent to which different sites with termites diverge from one another as a function of the environmental characteristics. Thus, when classified according to (i), the analysis of variance of the discriminant function Hotelling's T^2 test was significant ($\alpha = 0.05$) (Table 1), and soil water holding capacity (−1.5 MPa), cation exchange capacity, organic matter content, and base saturation were significant variables with discriminant loadings above ±0.9.

When sites were grouped according to (ii), the analysis of variance of the Hotelling's discriminant function were also significant but a different pattern emerged (Table 1). *Nasutitermes* spp. occurred in savannas with lower accumulation of aboveground phytomass, soils with less organic matter content, and lower cation exchange capacity as compared to sites where they were absent.

The same data showed distinctly different trends when grouped according to (iii) (Table 1). Sites where *Velocitermes* was present were characterized by a lower sand percentage (compare 60 vs 78%), and a higher clay percentage (22 vs 13%), water holding capacity (−8.0 vs −5.0 MPa), and base saturation (35 vs 59%). The aboveground phytomass was significantly higher in savannas with *Velocitermes* (448 g m^2) as compared to sites with *Nasutitermes* spp. (279 g m^{-2}).

DISCUSSION

The two groups of sites classified by the presence of *Velocitermes* and *Nasutitermes* at the Trachypogon savannas were mutually exclusive. One exception to this trend occurred at the EBLL where these two genera of termites were coexisting.

The occurrence of termite mounds in the Trachypogon savannas as a function of environmental characteristics (Table 1) can best be understood by first granting the primary importance of moisture as a limiting factor in survival, and then considering the particular strategies that termites have developed to cope with either the paucity of water during the dry season or temporary excess of water after heavy rains. Thus a critical period in the life of a colony occurs during the first year when its small size makes it most vulnerable to water stress. Colonies are normally established early in the rainy seasons when the

TABLE 1. *Multiple discriminant analysis of the occurrence of mound-building nasute termites as function of environmental attributes in Trachypogon savannas of the Orinoco Llanos (N = 26 sites).*[a]

Variable (mean ± SD)	*Nasutitermes*			*Velocitermes*			*Nasutitermes* and/or *Velocitermes*		
	Present (N = 10)	Absent (N = 16)	Discriminant loading	Present (N = 6)	Absent (N = 20)	Discriminant loading	Present (N = 15)	Absent (N = 11)	Discriminant loading
1. Sand (percent)	79.5 ± 13.8	69.7 ± 21.5	0.295	59.6 ± 14.5	77.7 ± 18.7	−0.743	72.1 ± 17.4	75.4 ± 22.1	−0.467
2. Clay (percent)	11.7 ± 7.4	17.0 ± 10.6	−0.681	22.4 ± 7.1	12.7 ± 9.4	0.960	15.6 ± 9.1	14.2 ± 10.9	0.037
3. Water holding capacity (−1.5 MPa)	4.6 ± 2.8	5.9 ± 3.7	0.681	8.0 ± 2.8	4.6 ± 3.2	−0.210	5.9 ± 3.3	9.8 ± 3.5	0.999
4. Ineffective mass of soil (>2 mm) percent	37.0 ± 31.0	54.0 ± 28.0	−0.823	32.0 ± 18.0	52.0 ± 32.0	0.416	34.0 ± 27.0	66.0 ± 24.0	−0.984
5. Infiltration rate (mm day^{-1})	9.01 ± 18.4	34.6 ± 50.7	−0.327	54.7 ± 63.7	15.7 ± 31.1	0.765	27.8 ± 47.0	20.5 ± 38.6	0.438
6. Cation exchange capacity (meg/100 g)	0.19 ± 0.24	0.69 ± 0.76	−0.751	0.69 ± 0.70	0.46 ± 0.66	0.307	0.35 ± 0.51	0.69 ± 0.80	0.998
7. Base saturation (percent)	64.3 ± 20.3	47.2 ± 22.3	0.880	35.8 ± 19.7	59.2 ± 21.2	−0.512	52.7 ± 24.6	55.3 ± 21.1	0.958
8. Soil organic matter (percent)	0.8 ± 0.8	1.3 ± 0.9	−0.800	0.9 ± 0.9	1.1 ± 0.8	0.380	0.8 ± 0.7	1.6 ± 0.8	−0.990
9. Above ground phytomass (g m^{-2})	279.2 ± 125.2	309.5 ± 155.1	−0.946	448.0 ± 111.0	252.8 ± 119.3	0.645	327.6 ± 135.3	257.2 ± 48.3	−0.898
F	3.23[b]			3.95[b]			3.52[b]		

[a] N = Number of sites.
[b] Significant, variance of discriminant function Hotelling's T^2 test ($\alpha = 0.05$) (Snedecor & Cochran 1967; Hair *et al.* 1984).

first downpours provide an external stimulus which synchronizes the release of alates. However, heavy rains are also dangerous to a newly formed pair or young colony which could be washed out by runoff or drowned.

This hypothesis may explain why the presense of *Nasutitermes* spp. but the absence of *Velocitermes,* on well-drained soils requires further study. Differences in the size of soil particles and the mound construction must be taken into consideration in order to understand why these two nasutitermites usually do not coexist in the same habitat. Thus, to construct the nest, termites seem to select the size of soil particles. The *Nasutitermes* spp. use sandy particles to construct their termitaria, and workers employ considerable amounts of fecal material as cement, visible as the dark material surrounding individual grains and lining galleries. By contrast, *Velocitermes* inhabits savannas with higher aboveground phytomass and use standing grass stems to support mounds. The walls of the *Nasutitermes* mounds are very crumbly and appear to be almost unelaborated soil (Coles de Negret & Redford 1982; Stansly, unpublished data). Therefore, soil texture seems to be the critical environmental requirement for mound building species, as shown by the studies of Roy-Nöel (1974) on termite species richness at Cap Vert Peninsula.

Another means both types of termite employ to avoid being either washed out or drowned is to take advantage of naturally occurring microrises in terrain. For this reason there is often an association between termite mounds and leafcutter ant mounds. Data taken from a relatively well-drained field (0.77 1 hr^{-1}), 5 km SE of Calabozo, will serve to illustrate the point. Along five transects (5 m wide and 50 m long) mounds were found in 1132 plots (1 m^2 each), with *Nasutitermes* spp. occurring on top of mounds of *Acromyrmex* sp. (Attini) 38 times while only 11 termite mounds and 33 ant mounds occurred alone. Given that 118 m^2 contained neither ant nor termite mounds, the probability of such a distribution occurring by chance is $P > .0001$ (χ^2 test). *Velocitermes* mounds may also be found on mounds of *Atta* spp. and also more consistent is their presence on raised portions of large grass clumps. At EBLL the grass *H. rufa* with large tufts of thick, tough culms probably offers especially good protection. This association between termite and ant mounds also occurs in Trachypogon Colombian savannas on Aquidystropept soils, which are temporarily flooded (Galvis *et al.* 1978) and between *Trinervitermes* mounds and ant hills in Sudan (R. H. Cowie, unpubl. obs.).

Termites face the opposite problem during the dry season, when the low water holding capacity of the savanna soils could be an unfavorable factor for surviving drought. Here again, the different strategies of *Velocitermes* and *Nasutitermes* spp. are evident. Thus the measurements of the water holding capacity at each site indicate that the finer textured soils, where the former are found, retain more moisture than the coarse soils in which *Nasutitermes* spp. occur. Consequently, one would expect *Nasutitermes* spp. to require easier access to deep-lying, sub-surface moisture to survive the dry season, as has been reported for *Psammotermes* sp. and *Macrotermes bellicosus* in West Africa (Grasse & Noirot 1948, 1961; Lepage 1974). This would explain why we did not find *Nasutitermes* spp. on the Guanipa highplains (Central Venezuelan Llanos) where the size of soil particles increase with soil depth in such way that less water is held in the profile. *Nasutitermes* mounds were found after descending the plains (Mesa) to the south of the Orinoco Llanos (Monagas), where soil texture is relatively uniform. On the other hand, *Velocitermes* is found in pockets of fine soil present in the cracks of the outcrop of indurated cuirasses at elevated sites such as hills of Tucucipano (Guárico State) and San Diego de Cabrutica (Anzoategui State), where the soil in these cracks is damp from the soil surface to the ground water table. Nonetheless these stony soil sites show less water loss by evaporation as compared with sandy soil (San Jose *et al.* 1985). It would appear that these mound-constructing termites seem to inhabit successfully the Trachypogon savannas by either withstanding stressful conditions in superficial soils with a relatively higher holding capacity, and/or less loss of water by evaporation, or avoiding these stressful conditions in a deeper soil profile by vertical migrations to layers with a higher water content. Similar observations have been reported for termite species in northern Senegal and Kenya (Josens 1983).

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