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Please cite as:

Martius, C., P.M. Fearnside, A.G. Bandeira and R. Wassmann. 1996. Deforestation and methane release from termites in Amazonia. Chemosphere 33(3): 517-536.

DOI: 10.1016/0045-6535(96)00201-9

ISSN: 0045-6535

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DEFORESTATION AND METHANE RELEASE FROM TERMITES IN AMAZONIA

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21 September 1993
21 Sept. 1993 SW
5 Dec. 1993
11 Dec. 1993
13 Dec. 1993

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Abstract

We re-evaluate the hypothesis that deforestation leads to higher termite populations and to a significant increase of methane release from termites in areas of cleared and burned former primary rain forest. Calculations are based on available information on population size, consumption, and methane emissions of Amazonian termites.

Termite species numbers are reduced after slash-and-burn, and their species composition changes to a predominance of more generalist, heat- and drought-resistant species. According to literature values, termite population biomass is 10.1 - 42.5 kg·ha⁻¹ in primary forest; it rises to 97.0 kg·ha⁻¹ in a six-year-old pasture, and falls to 2.1 kg·ha⁻¹ in a ten-year-old pasture. However, no significant difference exists between the mean of the primary forest populations and that of pasture populations modeled over a ten-year period on the basis of these data. No particular increase of wood-feeding species can be observed.

Calculated total consumption of pasture populations is 3.6 times that of termite communities in undisturbed primary forest. The population model data and different high-end wood consumption rates of termites (49 mg·g termites⁻¹·day⁻¹) allow for only 4.4% of the wood biomass left after burning to be decomposed by termites within ten years. These calculations suggest that an increase of methane emissions due to increased wood consumption in pasture is unlikely to occur.

The changes of methane emission rates due to termite population dynamics generated by deforestation were calculated for Amazonia as a whole on the basis of deforestation rates, methane emission rates, and termite populations. According to this, in 1990 termites in clearings in Brazilian Amazonia contributed $9.5 \cdot 10^{-3}$ Tg of CH₄ to ten-year cumulative net emissions (a measure of the long-term impact of the clearing done in a single year), or 0.02% of the 45 Tg CH₄·year⁻¹ annual increase in the atmospheric load of methane. In terms of the annual balance of net emissions (a measure of the impact in a given year of all present and past clearing activity), termites contributed $18.2 \cdot 10^{-3}$ Tg CH₄·year⁻¹, or 0.04% of the annual global increase.

1. INTRODUCTION

The atmospheric concentration of methane has been increasing at a rate of about $1\% \cdot \text{year}^{-1}$ (Dianov-Klokov et al., 1989, Khalil and Rasmussen, 1990, Wallace and Livingston, 1990, Badr, 1991, Crutzen, 1991). Recently the increase has been less rapid (Khalil and Rasmussen, 1993). The reasons for the enhanced abundance of methane in the atmosphere are not fully understood.

The general consensus as reported by the Intergovernmental Panel on Climate Change (IPCC) (Watson et al., 1990, 1992) is that agricultural activities such as rice cultivation and ruminant animal production contribute actively to the increase of this greenhouse gas. The hypothesis that termites significantly contribute to the global methane budget was first raised by Zimmerman et al. (1982), who estimated that these insects could be contributing approximately 30% of the global source strength of methane. These authors considered changes in the termite population resulting from deforestation as a major factor in the observed increase of atmospheric methane. Zimmerman et al. (1982) assumed rates of wood consumption and methane emission higher than those indicated by recent data (e.g. Khalil et al., 1990, Martius et al., 1993).

One important argument of Zimmerman et al. (1982) was that clearing of tropical forest and its conversion to pasture and agricultural land would increase termite density, and hence, methane emissions. However, the available data do not corroborate the assumption that termite populations could expand sufficiently to consume the wood that becomes available to them in the years following deforestation. Collins and Wood (1984) have shown for various sites in Sarawak, Nigeria, and Japan that forest clearing always (with one exception) reduces termite populations. It remains unclear whether this finding can be applied to other locations, such as Amazonia, where more than half of the world's rain forests are found. Evaluations of possible changes in the methane release should take into account changes in species composition; recent studies have revealed pronounced differences among Amazonian termite species with different food sources (Martius et al., 1993). In the present paper we will use the available data on termite population dynamics, wood consumption, and methane emission rates from

Brazilian Amazonia to evaluate the contribution of methane release from termites in deforested areas to the increase in global methane concentrations in the atmosphere.

2. RESULTS AND DISCUSSION

2.1. Quantifying deforestation and biomass left after burning

Amazonia is a six-country region of roughly $580 \cdot 10^6$ ha, originally 90% covered by forest (Leopoldo et al., 1985, Schubart, 1983). The original forest cover was approximately $522 \cdot 10^6$ ha. Brazil's Legal Amazon region (a nine-state administrative region within which special incentives for development apply) is $500 \cdot 10^6$ ha in area, $379 \cdot 10^6$ ha of which was originally forested (Fearnside and Ferraz, nd). Fearnside et al. (nd-a; see Fearnside, 1993a) recently determined that deforestation through 1990 (a base year often used for greenhouse gas emission calculations) had removed $41 \cdot 10^6$ ha, leaving $338 \cdot 10^6$ ha or remaining forest; the annual deforestation rate was $1.38 \cdot 10^6$ ha \cdot year $^{-1}$ in 1990 and $1.11 \cdot 10^6$ ha \cdot year $^{-1}$ in 1991.

The amount of dead wood mass which remains on the newly cleared land after burning was calculated on the basis of the following assumptions: the average total forest biomass (stems, roots, and leaves, including dead material) in forest areas cleared in Brazilian Amazonia 1990, after adjustment for logging removals, was 365 t \cdot ha $^{-1}$ (Fearnside, nd-a,b). Of this, 281 t \cdot ha $^{-1}$ is above-ground biomass, of which 182 t \cdot ha $^{-1}$, remains as wood after burning (Fearnside et al., 1993; Fearnside et al., nd-b,c). We assume that this is mainly heartwood, which is particularly hard and decay-resistant due to secondary metabolites present in the wood (Klocke and Kubo, 1991, Bustamante, 1993). The softer and smaller twigs and branches are more susceptible to fire, and mostly disappear with the burn (Fearnside et al., 1993).

2.2. Termite population dynamics after disturbance

The immediate, middle- and long-term responses of termite populations to disturbance (i.e., deforestation) must be differentiated; they can be qualitative (change in species composition) and quantitative (change in termite biomass). As

there are no studies accompanying the conversion of forest to pasture in the first years, we rely on biological assumptions to evaluate the development of the termite population in this critical phase. Tree-dwelling species are immediately affected by the logging, however, soil-dwellers may not be directly influenced on plots which are only logged but not burned. The dramatic microclimatic changes caused by deforestation make it clear that only those subterranean termites which are able to resist increased heat and dryness will survive. Logging and burning together is likely to reduce termite populations more sharply, and although some soil- or dead-wood dwellers may be sufficiently protected in their nests to survive the fire, the establishment of a new population will depend largely on colony-founding "royal" pairs of sexually mature alates, which must immigrate from adjacent areas. Colonizing flights of most termite species are restricted to a narrow period of the year (Nutting, 1969), the flight range of the alates is limited (Mill, 1982), and generally a considerable proportion of alates perishes due to predation during and after the flight (Wood and Sands, 1978). Termite life history traits in general suggest a true K-selection of population size with poor dispersal powers (Deshmukh, 1986); consequently, recolonization of burned areas is slow.

The physical density and the palatability of the wood both influence the feeding habits of termites and thus can affect their diversity on burned spots. Carbonized wood seems not to be attractive (C. Martius, unpubl. observation). Nasutitermes spp. prefer wood of low density; high-density wood is attacked only after previous conditioning by fungi (Martius, 1989, Bustamante, 1993). Rhinotermitidae attack only very strongly pre-decayed wood, and sampling of termites from decaying wood in a forest (C. Martius and A.G. Bandeira, unpubl. observation) showed that they seem to prefer the softer and more palatable twigs and branches (small dead wood). As almost only large boles are left on burned places, termites will not find much palatable wood to consume.

Middle-term population dynamics of termites can be evaluated from comparisons between primary forest and 1-ha forest patches which had been isolated from the contiguous forest for six years at the time of the study of Souza (1989; see Table 1). The total number of termite species and particularly the number of humivorous, soil-dwelling Apicotermatinae was reduced, and the relative frequency of arboreal nests in the samples was lower,

whereas the number of wood-dwellers (Cylindrotermes spp. - dry wood termites) and wood-feeding (though generally not wood-inhabiting) Nasutitermes spp. had increased in comparison with the contiguous areas. Heterotermes spp., which prefer moist rotten wood, were completely lacking, a fact attributed to the increased dryness in the small forest patches which are more affected by winds. Heat, wind and dryness are likely to have much more dramatic effects on termite populations when the forest cover is completely eliminated.

(Table 1 here)

What happens over the long term? Bandeira (1978, 1979) compared termite populations in primary forest and six-year-old pasture (pasture-6) in central Amazonia (Table 2), and Bandeira and Torres (1985) compared primary forest with a ten-year-old pasture (pasture-10) in eastern Amazonia (Table 3). Both studies were conducted on clayey to slightly sandy soil (Ultisol, or yellow latosol), the most abundant soil type of the region. The original data, which suffered from several shortcomings, were adjusted according to comments made by A.G. Bandeira (unpubl.; see footnotes to Table 2). The original values, not the corrections, were used for biological interpretation of the data; corrections are used for calculations of consumption and methane flux only.

(Tables 2 and 3 here)

The calculated total termite biomass in forest in central Amazonia ($42,484 \text{ g}\cdot\text{ha}^{-1}$) is about four times that in eastern Amazonia ($10,200 \text{ g}\cdot\text{ha}^{-1}$). This reflects the high diversity and variability of termite populations throughout Amazonia. We emphasize the great uncertainty concerning the average biomass of termites in the original forest, the value used here ($26.3 \text{ kg}\cdot\text{ha}^{-1}$) being the mean of these two highly divergent estimates. For the sake of our calculations, the data from forest and pasture can be arranged into a time sequence: Primary forest (average of both studies) - pasture-6 - pasture-10.

On clay soil in central Amazonia, termite nests (and calculated biomass) doubled from primary forest to pasture within six years after cutting (Table 2). In eastern Amazonia, individual numbers were drastically reduced to 15% of the forest values, and calculated biomass declined to one-fifth of the former population size (Table 3). In central Amazonia, the highest increase was for soil nests (which can belong to wood-feeders, soil-, and leaf-feeders; unfortunately, no separate account was made for wood-feeders). In eastern Amazonia, the reduction occurred in all fractions (termites in nests, dead wood, and soil), however the sharpest decline was for soil- and wood-dwelling termites.

In the latter study, all feeding guilds, independent of their feeding habits, suffered a reduction in species numbers (Table 4), indicating that probably only the most eurytopic species survived. The total number of species recorded in pasture is also below the 47-54 species found in the extremely diverse communities of the subtropical cerrado savannas in central Brazil (Egler, 1984, Domingos et al., 1986). Although no detailed account of the ecological requirements of the pasture species is possible, the numbers already indicate that pasture populations are different from those of natural savannas.

(Table 4 here)

In assessing methane emissions due to the hypothesized increase of wood-feeding termites in pasture, it is important to remember that, although wood mass increases suddenly after forest cutting, the wood is mostly unpalatable, and microclimatic conditions change so drastically that most forest termite species are unable to survive. In burned spots many termite colonies are destroyed by fire. The first wood-feeding Nasutitermes colonies were observed 1.5 years after burning (A.G. Bandeira, unpubl. observation). Nevertheless, termite populations in pasture, mostly soil-dwellers, recover so well within six years that their biomass is double that of forest populations. After ten years, however, termite populations had collapsed. As there is no dominance of wood-feeders in ten-year-old pasture, wood cannot be a major food source for termites at that stage.

The existing data allow termite population dynamics to be modeled, assuming linear changes between the existing measurements and assuming that the termite population in the first year after the burn is reduced to that observed in the ten-year-old pasture (Figure 1). The measured termite biomass values are indicated by symbols (squares) in Figure 1, and the assumed intervening changes by the solid line. It is theoretically possible that in the interval between the first and the sixth year termite populations could rise to a level much higher than that suggested by the pasture-6 values. However, the K-selected termite populations (see above) are unlikely to behave in this manner, and the model in Figure 1 is used in the following calculations.

(Figure 1 here)

The amount of above-ground biomass available to termites is shown in Figure 1. The decline after the initial peak is slightly irregular because, in addition to decay, the biomass is adjusted for losses in three re-burns over the ten-year period (Fearnside, nd-d) and for inputs of cut above-ground biomass from secondary forests (Fearnside, nd-c).

2.3. Consumption estimates of wood-feeding termites

The observed decrease in wood-feeding termites at pasture-10 could be interpreted as a consequence of having consumed all of the available wood by that time. We can then use consumption estimates together with population data to check whether the termites are really able to convert all that wood into CO₂ and CH₄. The few published estimates of termite consumption range between 6 and 270 mg wood·g termite⁻¹·day⁻¹ (Wood, 1978; data from 21 studies, recalculated from fresh to dry weight as in Table 3), and Wood and Sands (1978) calculated an average of 10 mg wood·g termite⁻¹·day⁻¹ from these data. In Amazonia, the consumption rate of the only species studied, Nasutitermes macrocephalus, is 49 mg wood·g termite⁻¹·day⁻¹ (Martius, 1989). We used this value together with the population biomass at each year indicated in Figure 1 to calculate wood consumption of the termites on pasture during the first ten years after deforestation. Consumption (and consequently emissions) are at all times limited by the size of

the termite population, rather than by the amount of dead wood biomass available to them. The fraction of wood consumed by termites is therefore independent of the consumption per termite in these calculations. Termites remove only $8.0 \text{ t wood}\cdot\text{ha}^{-1}$ within ten years after cutting, corresponding to 4.4% of the $182 \text{ t wood}\cdot\text{ha}^{-1}$ which were initially available. The calculated consumption of the pasture populations during ten years is only 6.3% higher than that of communities in undisturbed forest in the same period, whereas the input of dead wood due to forest burning is 7.4 times that of primary forests. In other words, the termite population would have to immediately increase by 39 times, and to persist at this level during the whole period to completely consume the $182 \text{ t}\cdot\text{ha}^{-1}$ within ten years. This is not compatible with any available information (Martius, 1989, 1993, nd). Termite populations play an important role in the turnover of organic matter in tropical ecosystems, but they are unable to react to sudden large litter inputs. Most of the wood available after burning will be slowly mineralized by fungi without any release of methane.

The available biomass in each year can be calculated from decay rates, yielding a decline as shown in Figure 1. The percentages of the available wood and of the wood decaying each year that can be ingested by the termite population are shown in Figure 2. Over the ten-year period following clearing, an average of 5.75% of the decay is mediated by termites. The percentage of decay mediated by termites is very low at the beginning and at the end of the ten-year period, and rises to a peak of about 15% between years 5 and 8 (Figure 2). The decay rates used to calculate this are smoothed by linear interpolation from rates over interburn intervals (shown in Figure 3) used in the emissions calculations; the smoothing avoids artifacts in the percent of decay mediated by termites (Figure 2). The decay rates for interburn intervals were derived by Fearnside (nd-c) from data of Buschbacher (1984) and Uhl and Saldariagga (nd).

(Figures 2 and 3 here)

For standing forest (Year "0" in Figures 1 and 2), biomass available is assumed to be the standing stock of coarse litter (16.4 t ha^{-1}) plus the annual production of fine litter (8.3 t ha^{-1})

¹) (see Fearnside, nd-c). Biomass available includes standing dead trees. The decay in standing forest is assumed to be the coarse litter decaying at the same rate as in first-year clearings (16.8% year⁻¹), plus all of the annual production of fine litter (Fearnside, nd-c).

2.4. Contribution of termites to the increase in atmospheric methane concentrations

An estimate of the termite contribution to the increase of atmospheric methane was obtained from calculating the methane emissions for termite populations of primary forest, pasture-6, and pasture-10, respectively, and balancing the differences in emissions from the total areas of primary forest and deforested land on an annual basis. Although it is possible that wood- and soil-feeders emit methane at different rates (Rouland, et al., 1993), the average emission rate for wood-feeders (Martius, et al., 1993) was applied to the total termite biomass of wood-, soil- and leaf-feeders. This emission of 3.0±1.3 ug hour⁻¹ is equivalent to 0.0023 tons of carbon released as methane per ton of carbon consumed (considering 50% carbon content of wood). This is virtually identical to the value obtained by Seiler et al. (1984) for termites in Africa. It is lower by a factor of four than the 0.0079 t methane C released/t wood C consumed estimated for Amazonian termites by Goreau and de Mello (1987). However, the lower value (Martius, et al., 1993) is believed to be more reliable, as higher value was based on monitoring a single nest for only two days, whereas the value used here is based on monitoring 15 nests for two years.

Two of the principal indices of greenhouse gas emissions are calculated in Table 5: cumulative net emissions and the annual balance of net emissions. Cumulative net emissions is one of the measures of the long-term impact of a land use change, such as the 1.38·10⁶ ha of deforestation that occurred in 1990. The annual balance of net emissions represents the net effect of emissions and uptakes in a single year from the entire landscape in the region (not just the area deforested in a given year). The annual balance includes prompt emissions and inherited emissions from land use changes in previous years (including termite-mediated decay of unburned biomass from prior clearings).

(Table 5 here)

The cumulative net emissions total $9.5 \cdot 10^{-3}$ Tg CH_4 , or only 0.02% of the global increase of $45 \text{ Tg CH}_4 \cdot \text{year}^{-1}$ (Crutzen, 1991). The change in the annual balance (as compared to the fluxes from the original forest prior to European colonization) represent $18.2 \cdot 10^{-3}$ Tg $\text{CH}_4 \cdot \text{year}^{-1}$, or 0.04% of the annual increase in the global atmosphere.

Considering the entire history of deforestation in Brazilian Amazonia (mainly accomplished in this century), annual net methane flux due to termites from the region changed from a calculated $9.84 \cdot 10^{-3}$ Tg $\text{CH}_4 \cdot \text{year}^{-1}$ (for $379 \cdot 10^6$ ha of primary forest) to $11.66 \cdot 10^{-3}$ Tg $\text{CH}_4 \cdot \text{year}^{-1}$ (Table 5). In the same period, methane concentrations in the atmosphere almost doubled, from 900 ppb around the year 1900, to 1700 ppb today (Raynaud, 1993). Methane emissions from termites in Brazilian Amazonia therefore make only a negligible contribution to the global methane budget.

3. CONCLUSION

The lack of reliable data on termite populations in tropical forests is lamentable, and we are still far from understanding the dynamics of arthropod populations following forest conversion. More detailed measurements are needed to understand the factors which control methane emission from termites and methane oxidation by methanotrophic bacteria on the nest walls and in the soil, and to balance both processes. Nevertheless, the present state of knowledge permits us to conclude that termite population changes following deforestation do not play a significant role in the increase of global atmospheric methane concentrations.

ACKNOWLEDGMENTS

This study was supported by a grant from Max-Planck Institute for Limnology, Work Group in Tropical Ecology, Plön, Germany, and received technical support from Fraunhofer-Institut für Atmosphärische Umweltforschung, Garmisch-Partenkirchen,

Germany. The Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil, provided logistical facilities for the studies. A.G. Bandeira received a grant from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Brasília.

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Table 1: Numbers of termite species in areas of contiguous forest and isolated forest patches of different size in central Amazonia

Size of Study Area	Contiguous Forest	Isolated Forest Patch
10 ha	75 (11)	50 (3)
1 ha	40 (7)	13 (1)

1. Data from Souza (1989). Values in parenthesis indicate number of Anoplotermes species only.

Table 2: Termites in primary forest and six-year-old pasture in central Amazonia

Termite density measure	Fraction Forest	Primary	6-year-old Pasture
Nests Arboreal (nests·ha ⁻¹)	36	52	
Soil Nest		64	152
TOTAL	100		204
Population (individuals·m ⁻²) ¹⁾	Arboreal	398	575
	Soil Nest	2,472	5,869
TOTAL		2,870	6,444
Biomass (g·ha ⁻¹) ^{2,3)}	Arboreal	4,020	5,810
	Soil Nest	29,954 ⁴⁾	79,598
Dead Wood Ground		7,560 ⁵⁾	11,500 ⁷⁾
Standing Dead Wood		950 ⁶⁾	70 ⁸⁾
TOTAL		42,484	96,978

1. Calculated from original values of Bandeira (1978) with modifications described in the footnotes that follow. Original values indicate only nest numbers. Population density (individuals·m⁻²) was calculated from the average value of 110,600 individuals·nest⁻¹ (Bandeira and Torres, 1985).

2. Biomass calculated from individual numbers using the average value of 1 mg/individual (Martius, 1989).

3. Immature "nymphs" originally not counted. According to Martius (1989), in young nests nymphs account for 12% of the individuals, and immature ("white") soldiers for 5%; both are at almost 0.0% in old nests. Biomass of nymphs and white soldiers is 0.1 and 0.3 g·individual⁻¹, respectively. Young nests account for 35%, and old

ones for 65% of the nest population. Thus, the original numbers were increased by $0.12 \cdot 0.35 \cdot 0.1 = 0.3\%$ for nymphs, and by $0.05 \cdot 0.35 \cdot 0.3 = 0.7\%$ for white soldiers. (In total 1.0% was added).

4. Soil fauna was originally assessed only to a depth of 5 cm. As only 24% of all termites found in the top 30 cm of soil by Harada and Bandeira (nd) occurred in the 0-5 cm range in forests with clay soils near Manaus, the number of termites in the 0-30 cm depth range was recalculated from the original numbers using this percentage. The vertical distribution of termites in the soil represents a major source of uncertainty in the present calculations. For example, Adis and Ribeiro (1989: 119) found that 80-90% of all soil arthropods occurred in the 0-7 cm range, implying that the biomass of soil termites should only be increased over the original 0-5 cm measurements by about 20% (which would reduce the soil termite population in forest in central Amazonia and in six-year-old by an order of magnitude and the total termite population at these sites by approximately a factor of two).

5. Dead wood from the forest floor was not sampled in central Amazonia. As it accounts for 60% of the total termite biomass sampled in eastern Amazonia, 60% of the total biomass was added, assuming that termite biomass is a linear function of dead wood weight.

6. Standing dead wood was not sampled in both studies (see Table 3). Standing dead wood accounts for 25% of total dead wood (Fearnside, nd-c); however, it is generally much drier than dead wood on the ground, which has negative effects on termites in the wood (reduction estimated at 50%); consequently $0.25 \cdot 0.50$ or 12.5% were added to the total termite population in both studies.

7. For pasture, the termite population within dead wood was reduced to 67% of the original value, as this is the wood volume left after deforestation.

8. Only very few dead boles are left standing on a burned pasture (estimated to be 5% of the original standing dead wood). Thus, $0.05 \cdot 0.125 = 6\%$ was added.

Table 3: Termites in primary forest and ten-year-old pasture in eastern Amazonia

Termite density measure	Fraction	Primary	10-year-old	Forest	Pasture
Population (Individuals $\cdot m^{-2}$) ¹⁾	Nests	290	120		
	Soil 0-15 cm	1,230		130	
	Fallen dead Wood	350		30	
TOTAL		1,870	280		
Biomass (g $\cdot ha^{-1}$)	Nests ^{2,3)}	2,910	1,230		
	Soil 0-15 cm ^{4,3)}			510	100
	Fallen Dead Wood ^{4,3)}	6,030		770 ⁵⁾	
	Standing Dead Wood	750 ⁶⁾		10 ⁷⁾	
TOTAL		10,200	2,110		

1. Original data from Bandeira and Torres (1985), corrected according to the footnotes that follow.

2. Dry weight (DW) calculated from fresh weight (FW) using $DW=FW/3$ (Martius, 1989, Wood and Sands, 1978).

3. Corrected for nymphs as explained in Table 2, footnote 3.

4. Calculated using $1 \text{ mg}\cdot\text{individual}^{-1}$ (Martius, 1989).

5. Corrected for reduction in wood mass available, cf. Table 2, footnote 7.

6. Corrected for standing dead wood (cf. Table 2, footnote 6).

7. Standing dead wood calculated as in Table 2, footnote 8.

Table 4: Numbers of termite species per hectare according to feeding guilds in primary forest and ten-year-old pasture in eastern Amazonia

Feeding Habit	Primary Forest	Ten-Year-Old Pasture
Wood-Feeding	34	18
Intermediate	15	7
Humivorous	14	7
TOTAL	63	32

1. Same study plots as in Table 3. Data from Bandeira (1989).

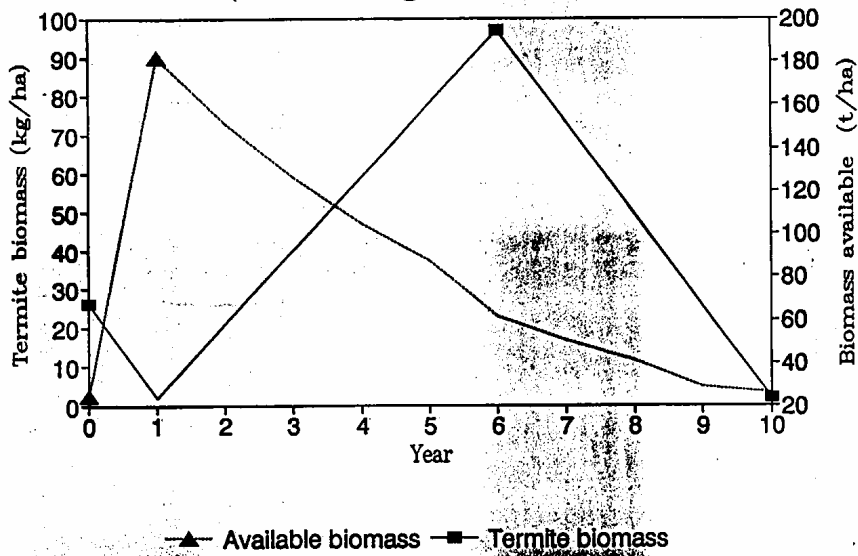
FIGURE LEGENDS

Figure 1 - Termites and available wood biomass following clearing in Brazilian Amazonia.

Figure 2 - Consumption of biomass by termites, expressed as percent of available biomass consumed (solid line) and percent of decay mediated by termites (dotted line).

Figure 3 - Decay rates for original forest biomass, showing annual rates applying over interburn intervals (triangles) and smoothed rates interpolated from these (solid line).

TERMITES AND AVAILABLE BIOMASS (dead above-ground biomass)



CONSUMPTION OF BIOMASS BY TERMITES

