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Effect of underground fungus-growing termites on carbon dioxide emission at the point- and landscape-scales in an African savanna

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Summary

1. The rate of CO_2 emission by two major termite species (*Ancistrotermes cavithorax* and *Odontotermes n. pauperans*) was studied in a West African savanna (Lamto, Côte d'Ivoire). First, in three major savanna types (grassy, shrubby and woody savannas), CO_2 emission from the soil surface was measured using a closed container system. Control soil without termite fungus-comb chambers, and soil of eroded termite mound with or without *Odontotermes* fungus-comb chambers was sampled in each savanna type. Second, the mass-specific respiration rate of the different components of termite fungus-comb chambers (i.e. workers, soldiers, fungus comb and chamber walls) was measured under laboratory conditions. CO_2 emission by termites at the landscape-scale was computed from both field biomass data and laboratory measurements.

2. Whatever the savanna type, CO_2 emission from the soil surface was not different between control soil and soil of eroded termite mound without termite fungus-comb chambers, but was significantly higher in areas with fungus-comb chambers than in areas without fungus-comb chambers (10–19 μmol CO_2 m^{-2} s^{-1} *vs* 5–10 μmol CO_2 m^{-2} s^{-1}).

3. The mass-specific respiration rates were higher for individuals of *O. pauperans* than for individuals of *A. cavithorax*. Total respiration rate from an individual fungus-comb chamber was around 56 and 143 μmol CO_2 h^{-1} for *Ancistrotermes* and *Odontotermes*, respectively.

4. Despite a low mass-specific respiration rate, fungus comb accounted for 51% of the total respiration flux from whole chambers in *Odontotermes* and for 82% in *Ancistrotermes*. The laboratory-derived respiration rate from individual *Odontotermes* chambers was consistent with the field estimates.

5. At the landscape-scale, the CO_2 emission due to *A. cavithorax* and *O. pauperans* was 0·022 and 0·050 μmol CO_2 m^{-2} s^{-1}, respectively. This total (27·2 g C m^{-2} $years^{-1}$) represented 4·9% of the total above-ground net primary production in this ecosystem and 11·3% of the carbon not mineralized by annual fires.

Key-words: Carbon cycle, Côte d'Ivoire, Guinean savanna, Macrotermitinae

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Introduction

In tropical regions, termites influence the structure and functioning of ecosystems in several ways. First, termites strongly modify soil texture and structure (Lee & Wood 1971; Lobry de Bruyn & Conacher 1990; Konaté *et al.* 1999; Holt & Lepage 2000). Secondly, they can have a huge impact on carbon cycling by processing large quantities of plant material (Wood & Sands 1978; Josens 1983). This is particularly true for the Macrotermitinae subfamily, species of which form an obligate exosymbiosis with the fungus *Termitomyces*. For instance, 1·4 tonnes of litter per hectare and per year are consumed by termites in certain Malaysian forests according to Matsumoto & Abe (1979), and 90% of dead wood was

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found to be degraded by termites in a semi-arid savanna in Kenya (Buxton 1981). In the humid savanna of Lamto in Ivory Coast, termites use about 27% of the annual litter production (Josens 1983).

Some studies have suggested that termites are a major cause of carbon depletion in semiarid and arid soils (Holt 1987; Jones 1990). The work of Zimmerman *et al*. (1982) highlighted the potential role of termites as a source of atmospheric trace gases. However, following this contribution, a debate stirred the scientific community about the exact contribution of termites to global emissions of greenhouse-forcing gases, notably CH_4 (Khalil & Rasmussen 1983; Collins & Wood 1984; Seiler *et al*. 1984; Zimmerman *et al*. 1984; Fraser *et al*. 1986). Several recent detailed studies have closed the debate, proving that the actual termite contribution to gas fluxes remained small in the global context (Bignell *et al*. 1997; MacDonald *et al*. 1998, 1999; Eggleton *et al*. 1999; Jeeva *et al*. 1999; Sugimoto *et al*. 2000).

Most of these studies focused on methane and carbon dioxide emissions from forest ecosystems (Khalil *et al*. 1990; Lawton *et al*. 1996; Bignell *et al*. 1997; Nunes *et al*. 1997; Curtis & Waller 1998; MacDonald *et al*. 1998, 1999; Eggleton *et al*. 1999; Jeeva *et al*. 1999), and arid or semi-arid savanna ecosystems (Zimmerman *et al*. 1984; Holt 1987; Jones 1990; Darlington *et al*. 1997). Fewer studies concerned the humid savanna; carbon fluxes in this biome are poorly understood and carbon budgets are often not balanced. Data available reveal some differences in flux assessment between laboratory and field measurements (Khalil *et al*. 1990). In addition to potential biases in flux measurements, a main difficulty results from the lack of reliable estimation of termite populations in the field.

In this context, the humid savannas of Lamto Natural Reserve (Côte d'Ivoire) offer a unique opportunity to study the effect of termites on CO_2 emissions from soils at the landscape-scale, as termite density is well documented (Josens 1972, 1974, 1983; Konaté 1998). There is a good knowledge of the nest structure of two major fungus-growing species, *Ancistrotermes cavithorax* (Sjöstedt) and *Odontotermes n. pauperans* (Silvestri). Their nests are made of individual underground fungus-comb chambers within the soil profile, interconnected with galleries. *Ancistrotermes* builds diffuse nests in the various savanna environments, while chambers of *Odontotermes* are mostly concentrated into termite mounds of various sizes. The occurrence of such mounds is a characteristic feature of the Lamto savanna (Abbadie *et al*. 1992; Konaté 1998) and the mounds deeply modify soil properties and vegetation structure (Abbadie *et al*. 1992; Le Roux *et al*. 1995; Konaté *et al*. 1999).

The objectives of this paper are: (1) to characterize the respiration rates of the different components of termite fungus-comb chambers (i.e. workers, soldiers, fungus comb and chamber walls) for *A. cavithorax* and *O. pauperans* under laboratory conditions; (2) to document the influence of *Odontotermes* fungus-comb chambers on soil respiration in the field in different savanna types; (3) to compare field and laboratory measurements of CO_2 emissions from individual fungus-comb chambers of *Odontotermes;* and (4) to assess the influence of *A. cavithorax* and *O. pauperans* on CO_2 emission from soils at the landscape scale.

Materials and methods

THE LAMTO SAVANNA AND TERMITE NEST DENSITIES

The field measurements were carried out in the three savanna types in Lamto (grassy, shrubby and woody savannas), as described by Menaut & César (1979), from July to September 1995. There was a medium precipitation (271 mm with a total annual precipitation of 1156 mm, as compared with an average of 291 mm and 1210 mm for the 1962–95 period) and a constant monthly mean temperature ($27{\cdot}7 \pm 0{\cdot}2$ °C) during this period.

The two species, *Ancistrotermes cavithorax* and *Odontotermes n. pauperans* are dominant within the fungus-growing (Macrotermitinae) trophic group in this ecosystem and represent about 70% of the total trophic group biomass (Josens 1972).

The density of the termite nest units (fungus-comb chambers), the mass of the fungus-comb and the density of termite populations were assessed using the results obtained by Josens (1972, 1974, 1977) completed by field sampling made by Konaté (1998), to determine the density of the mounds in the landscape and the density of the fungus-comb chambers on the mounds and outside. Three parcels of 7·5 ha were delimited in each savanna type and divided into 30 plots of 50×50 m^2, subsequently divided into smaller plots of 25×25 m^2. In each plot, the mounds were mapped and their size measured. All the fungus-comb chambers in 18 mounds in the three savanna types were mapped, destructively sampled and attributed to each termite species. The sizes of the chambers were measured and the fungus-comb weighed. To sample the fungus-comb chambers in between the mounds, five quadrats of 625 m^2 were chosen at random in each parcel and subsampled by a network of 1×1 m^2 quadrats, up to 30 cm deep. The data obtained from 625 m^2 quadrats and from the mound sampling were averaged, taking into account the percentage of the area occupied by the mound bases (Konaté 1998).

Mean numbers of termite castes per fungus-comb chamber have been obtained from 10 quadrats of 1 m^2 thoroughly excavated according to the method previously described in Lamto (Lamotte & Bourlière 1969; Josens 1972). The total number of termites found was divided by the total number of the fungus-comb chambers found. Therefore, this method considered all the termites present in the soil volume, whether inside the chambers or outside. The larvae were not included in our data, as their small size hampered an accurate sampling.

FIELD MEASUREMENTS

In each savanna type, measurements were made between 10.00 and 15.00 hours, at soil temperatures ranging from 28 to 30 °C on termite mounds. Three termite mounds were sampled per savanna type. On each mound, eight measurements were made in locations where *Odontotermes* fungus-comb chambers were detected below the soil surface several days before the measurements, and eight measurements to one side of the chambers (at about 25–50 cm). In each savanna type, eight measurements were made in the surrounding savanna (10–20 m) to one side of termite chambers.

CO_2 emission from soil was measured with a closed container system and an infrared gas analyser (ADC LCA-2, Analytical Development Co., Hoddesdon, UK). A cylindric, 11-l chamber with a 0·06-m basal diameter (the mean diameter of *Odontotermes* fungus-comb chambers is 0·04–0·05 m) was used. Equilibration with the external atmospheric pressure was ensured by a pressure vent to reduce methodological biases (Livingston & Hutchinson 1995). The chamber base was inserted 5 cm into the soil surface to ensure airtightness. The soil-to-air net CO_2 exchange rate was determined from the variation in CO_2 concentration inside the chamber within a 3–5-min period after the beginning of the measurement. Linearity of the increase in CO_2 concentration was checked for each determination. Air CO_2 concentration within the chamber was always below 600 ppm at the end of the measurement period. Calibration of the gas analyser was checked in the field before and after each measurement period using a standard gas.

LABORATORY MEASUREMENTS

In the laboratory a nanorespirometer, which measures consumed oxygen (Verdier 1983), was used to assess the respiration rate per unit mass of individual components (termite individuals, fungus-comb and fungus-comb chamber wall) from 2-year-old incipient colonies of *Ancistrotermes cavithorax* and *Odontotermes n. pauperans*. Each measurement was made on three termite individuals at a time and on mixed fungus-comb samples (from different parts of the comb), sealed into a respirometer cell for automatic measurement. The temperature was constant (28 °C) and high air moisture was maintained using a moist filter paper. For each nest component, four replicates were used. The respiratory activity was expressed as nmol of O_2 consumed per mg dry mass of termite (or comb or wall) per hour. Since respiration quotient (i.e. the ratio between CO_2 emission rate and O_2 consumption rate) is very close to one for most of the Macrotermitinae (Collins 1977; Matsumoto 1977; Veivers *et al*. 1991; Darlington *et al*. 1997; Nunes *et al*. 1997), absolute values of oxygen uptake and carbon dioxide production were assumed to be equal.

COMPUTATION OF TOTAL RESPIRATION RATES FROM INDIVIDUAL FUNGUS-COMB CHAMBERS, AND COMPARISON OF LABORATORY AND FIELD DATA

For the calculation of respiration rate from individual fungus-comb chambers, the mass-specific respiration rate of each component (measured in laboratory) was multiplied by the total dry mass of each component per chamber (according to the field data given by Konaté 1998 and personal communication). For *Odontotermes*, these values were compared with values deduced from field measurements, while the respiration rate from one termite chamber (expressed as μmol CO_2 h^{-1}) was computed from the differences between values measured on eroded mounds in locations with *Odontotermes* fungus-comb chambers, and values measured on eroded termite mounds in locations without termite fungus-comb chambers. Excavations performed after each measurement showed that there was either zero or one chamber below the sampled areas. For computation, all the CO_2 produced by the termite fungus-comb chamber was assumed to leave the soil through the sampled area. This assumption gave a minimum value of chamber respiration because, even if the chamber was located immediately below the sampled area, some CO_2 produced by the termite chamber could leak out of the sampled area. Potential effects of other chambers located close to the sampled area were assumed to be negligible.

ASSESSMENT OF CO_2 EMISSION AT THE LANDSCAPE SCALE

To assess the CO_2 emission rate by the two termite species at the landscape scale, we first determined the emission rate for each zone (i.e. on or between mounds) in each savanna type. The calculated emission rate per fungus-comb chamber was multiplied by the chamber density on the termite mound or in the surrounding savanna previously determined in Lamto (Konaté 1998). Then, the mean CO_2 emission rate in each savanna type was determined according to the relative proportion of surface occupied by the mounds. Finally, the emission rate at the landscape scale was computed from the emission rates of the different savanna types and the relative proportion of each savanna type in Lamto reserve (Gautier 1989).

STATISTICAL ANALYSIS

Comparisons between field measurements of CO_2 emission for the different savanna and soil types were tested by the mean of STATISTICA (Statsoft-France 1997) MANOVA test with Tukey HSD (Honest Significant Difference) *post hoc* comparisons, to distinguish between the savanna type effect, the mound effect and their interactions. Non-parametric Kruskal–Wallis ANOVA was used to test differences between results from nest components in the laboratory.

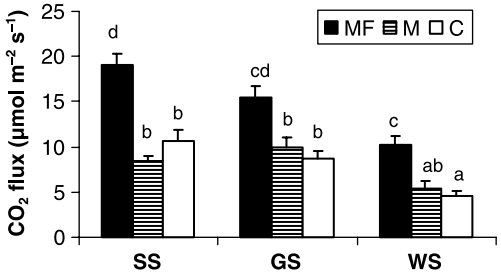

Fig. 1. *In situ* soil respiration rates measured in grassy (GS), shrubby (SS) and woody (WS) savannas, for control savanna soil (C), for locations without termite chambers on termite mounds (M) and for locations with *Odontotermes* fungus-comb chambers on termite mounds (MF). Bars are standard errors. Values with the same letter are not significantly different at the $P = 0{\cdot}05$ level (two-way ANOVA, $n = 9$).

Results

FIELD CO_2 EMISSION FROM SOILS WITHIN AND OUTSIDE *ODONTOTERMES* NESTS

In each savanna type, CO_2 fluxes from control soil and from locations without fungus-comb chambers on termite mounds were not significantly different (two-way ANOVA soil type × savanna type) (Fig. 1). Control soil respiration was significantly lower in woody savanna (around 5 µmol CO_2 m^{-2} s^{-1}) than in grassy and shrubby savannas (around 9 µmol CO_2 m^{-2} s^{-1}) ($P < 0{\cdot}05$, $n = 9$). In shrubby and grassy savannas, CO_2 fluxes from locations with *Odontotermes* fungus-comb chambers on termite mounds were significantly higher ($P < 0{\cdot}01$, $n = 9$) than emission rates from bulk mound soils (Fig. 1).

RESPIRATION RATES FROM ISOLATED NEST COMPONENTS

The comparison of the mass-specific respiration rates of nest components of *Odontotermes* and *Ancistrotermes* (non-parametric Kruskal–Wallis ANOVA test by ranks, Table 1) showed that (i) for a given termite species, the highest and lowest respiration rates were obtained for workers and chamber walls, respectively, whereas intermediate respiration rates were obtained for soldiers and fungus comb samples; (ii) whatever the species, the respiration rate of fungus-comb chamber walls (0·6–0·9 nmol mg^{-1} h^{-1}) was significantly higher ($P < 0{\cdot}05$, $n = 4$) than the respiration rate from control soil (0·13 nmol mg^{-1} h^{-1}); (iii) respiration rates of soldiers and workers were significantly higher in *Odontotermes* than in *Ancistrotermes,* whereas respiration rates from fungus combs did not differ between the two species (*ca.* 10 nmol mg^{-1} h^{-1}).

Table 1. Comparison between mass-specific respiration rates for the different components of the fungus-comb chambers of *Ancistrotermes cavithorax* and *Odontotermes n. pauperans.* Means are presented with standard errors. Values with the same letter are not significantly different at the $P = 0{\cdot}05$ level (Kruskal–Wallis test, $n = 4$)

	CO_2 flux (nmol mg^{-1} h^{-1})	
	Ancistrotermes cavithorax	*Odontotermes n. pauperans*
Major soldier	31·4 ± 0·2 (a)	52·1 ± 8·8 (b)
Minor soldier	51·6 ± 8·8 (b)	–
Major worker	62·1 ± 10·3 (b)	125·8 ± 18·3 (g)
Minor worker	83·9 ± 6·0 (c)	133·5 ± 22·3 (g)
Fungus comb	11·1 ± 0·3 (f)	10·0 ± 1·6 (f)
Chamber walls	0·60 ± 0·04 (e)	0·90 ± 0·05 (h)
Control soil	0·13 ± 0·00 (d)	0·13 ± 0·00 (d)

ESTIMATED RESPIRATION RATES FROM INDIVIDUAL CHAMBERS

According to Konaté (1998; and personal observation), the mean number of workers in a fungus-comb chamber of *Odontotermes* is 150 termites, corresponding to 82·8 mg dry mass. The mean dry mass of one comb is 7·25 g. Total mean respiration rate from a chamber of *Odontotermes* was thus estimated to be around 143 µmol CO_2 h^{-1} (Table 2a). Despite a relatively low mass-specific respiration rate, fungus-comb accounted for 50·8% of the total respiration flux from the whole chamber, while workers, soldiers and chamber walls represented 7·0%, 0·2% and 42·2% of total respiration, respectively (Table 2a).

Similarly, a fungus-comb chamber of *Ancistrotermes* contains a mean total of 110 termites, corresponding to 53 mg dry mass, and the mean dry mass of one comb is 4·1 g. An estimate of the total mean respiration rate from a chamber of this species would average 55·5 µmol CO_2 h^{-1}. Despite its relatively low mass-specific respiration rate, the fungus comb accounted for 82% of total respiration flux from the whole chamber. The workers, soldiers and chamber walls represented 6·5%, 0·3% and 11·2% of total respiration, respectively (Table 2b).

The comparison of CO_2 emission rates from termite mounds in locations with *Odontotermes* chambers and from mounds in locations without termite chambers showed an average emission rate from one chamber of 67·7, 151·6 and 80·9 µmol CO_2 h^{-1} in the grassy, shrubby and woody savannas, respectively (Fig. 2). These values were thus broadly consistent with the mean chamber respiration rate computed from laboratory measurements (142·8 µmol CO_2 h^{-1}).

CONTRIBUTION OF THE TWO TERMITE SPECIES TO THE CO_2 EMISSION AT THE LANDSCAPE SCALE

Our estimates of densities of fungus-comb chambers in Lamto took account of (i) fungus-comb chamber density on and between termite mounds, and (ii) the percentage of area covered by such mounds in three savanna types at Lamto (Table 3). The percentage of total area covered by termite mounds varied from 3 to

Table 2. Computation of CO_2 respiration rates per individual fungus-comb chamber of *Odontotermes n. pauperans* or *Ancistrotermes cavithorax*, obtained as the sum of the respiration rates of the chamber components. The mean number and mass of each fungus-comb chamber component in Lamto savanna was determined by Konaté (1998)

Chamber components	Individual dry mass (mg)	Mean number per chamber	Dry mass per chamber (mg)	Mass-specific rate (nmol/mg/h)	CO_2 flux (μmol h^{-1} chamber)
(a) *Odontotermes n. pauperans*					
Soldier	0·456	10·5	4·79	52·1	0·25
Major worker	0·720	79·5	57·24	125·8	7·2
Minor worker	0·346	60·0	20·75	133·5	2·8
Fungus comb	7 250	1	7 250	10·0	72·5
Chamber wall	66 759	1	66 759	0·90	60·1
Chamber total					142·8
(b) *Ancistrotermes cavithorax*					
Major soldier	0·384	5	1·9	31·4	0·06
Minor soldier	0·147	12	1·76	51·6	0·09
Major worker	0·404	56	22·6	62·1	1·4
Minor worker	0·158	37	26·3	83·9	2·2
Fungus comb	4 080	1	4 080	11·1	45·5
Chamber wall	10 557	1	10 557	0·59	6·2
Chamber total					55·5

Table 3. Densities of fungus comb chambers of *Ancistrotermes cavithorax* and *Odontotermes n. pauperans* in three savanna types of the Lamto savanna. For each savanna type, values were computed from (i) chamber densities on eroded mounds and in the surrounding areas, and (ii) the percentage of total area covered by mounds, both as measured by Konaté (1998)

Savanna type	Total area covered by mounds (%)	Termite species	Chamber density on mounds (m^{-2})	Chamber density out of mounds (m^{-2})	Mean chamber density (m^{-2})
Grassy savanna	5·3	*Ancistrotermes*	0·4 ± 0·1	0·4 ± 0·06	0·4 ± 0·08
		Odontotermes	7·8 ± 0·6	0·3 ± 0·05	0·7 ± 0·3
Shrubby savanna	2·9	*Ancistrotermes*	4·6 ± 1·1	1·5 ± 0·5	1·6 ± 0·7
		Odontotermes	17·6 ± 3·8	1·0 ± 0·1	1·5 ± 0·6
Woody savanna	4·0	*Ancistrotermes*	3·2 ± 0·1	4·0 ± 0·9	3·9 ± 1·1
		Odontotermes	12·4 ± 0·8	0·25 ± 0·1	0·7 ± 0·3

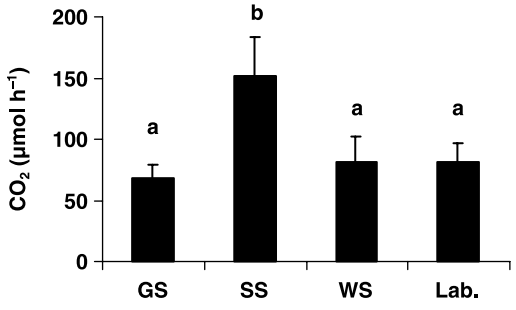

Fig. 2. Comparison between CO_2 flux produced by an individual *Odontotermes fungus-comb* chamber, as estimated from laboratory measurements (laboratory) or from CO_2 emission rates measured in the field in grassy (GS), shrubby (SS) and woody (WS) savannas. Bars are standard errors. Values with the same letter are not significantly different at the $P = 0·05$ level.

5% according to the savanna type. The fungus-comb chamber density of the two termite species varied according to the savanna type and to the presence or absence of mounds. Whatever the savanna type, the fungus-comb chamber density of *Odontotermes* on termite mounds (7·8–17·6 m^{-2}) was higher than that of *Ancistrotermes* (0·4–4·6 m^{-2}). In contrast, in the surrounding soil of woody and shrubby savannas, *Ancistrotermes* showed a higher fungus-comb chamber density (0·4–4·0 m^{-2}) than *Odontotermes* (0·25–1·0 m^{-2}). For the whole savanna (i.e. mound and surrounding zone), the fungus-comb chamber density of *A. cavithorax* was higher than that of *Odontotermes n. pauperans* in woody savanna, similar to each other in shrubby savanna, whereas the fungus-comb chamber density of both species was low in grassy savanna (Table 3).

Using (i) these field estimates of fungus-comb chamber densities, and (ii) the total respiration rates from individual chambers of *Odontotermes* and *Ancistrotermes* as estimated in the laboratory, we computed the CO_2 fluxes produced by fungus-comb chambers of these two termite species at the scale of each savanna type and at the landscape-scale in the Lamto region (Table 4). In the grassy savanna, where most of the termite activity is concentrated on mounds, CO_2 emission due to *Odontotermes* (28 nmol m^2 s^{-1}) was about five times higher than that due to *Ancistrotermes* (6 nmol m^2 s^{-1}). In the woody savanna, characterized by a higher density of *Ancistrotermes* fungus-comb chambers, the emission due to this species (60 nmol

Table 4. Estimated CO_2 emission rates from fungus-comb chambers of *Ancistrotermes cavithorax* and *Odontotermes n. pauperans* in different savanna types and at the landscape-scale at Lamto computed from (i) respiration rates per chamber estimated from laboratory measurements (Table 2), and (ii) estimated field chamber densities (Table 3)

Scale	Total area (%)*	Density of *Odontotermes* chambers (m^{-2})	CO_2 emission rate from *Odontotermes* chambers ($\mu mol\ m^{-2}\ s^{-1}$)	Density of *Ancistotermes* chambers (m^{-2})	CO_2 emission rate from *Ancistotermes* chambers ($\mu mol\ m^{-2}\ s^{-1}$)	CO_2 emission rate from chambers of the two species ($\mu mol\ m^{-2}\ s^{-1}$)
Grassy savanna areas	25·2	0·7	0·028	0·4	0·006	0·034
Shrubby savanna areas	70·9	1·5	0·059	1·6	0·025	0·084
Woody savanna areas	3·9	0·7	0·028	3·9	0·060	0·088
Lamto landscape	100	1·3	0·050	1·4	0·022	0·072

*According to Gauthier (1989).

Table 5. Comparison of mass-specific respiration rates of the fungus-comb chamber components (i.e. workers, soldiers and fungus combs) for different fungus-growing termite species (nmol CO_2 per mg dry mass per hour). Data for *Macrotermes* (forest and savanna species) were obtained from field measurements with adult nest and intact fungus combs, while data for *Odontotermes n. pauperans* and *Ancistrotermes cavithorax* were obtained from laboratory measurements on incipient colonies. Data are presented as mean ± standard error (number of observations)

	Mass-specific respiration rates ($nmol\ mg^{-1}\ h^{-1}$)				
	Macrotermes bellicosus at 30 °C (Collins 1977)	*Macrotermes carbonarius* at 29 °C (McComie & Dhanarajan 1990)	*Macrotermes jeanneli* at 32 °C (Darlington *et al*. 1997)	*Odontotermes* sp. at 28 °C (this study)	*Ancistrotermes cavithorax* at 28 °C (this study)
Minor worker	115·5 ± 30·2	67·2 ± 3·6	78·5 ± 7·0 (2)	133·5 ± 22·3 (4)	83·9 ± 6·0 (4)
Major worker	69·4 ± 13·8	47·1 ± 7·8	76·0 ± 11·3 (4)	125·8 ± 18·3 (4)	62·1 ± 10·3 (4)
Minor soldier	98·7 ± 33·3	35·5 ± 12·0	76·0 ± 8·1 (2)	–	51·6 ± 8·8 (4)
Major soldier	52·3 ± 20·8	15·1 ± 2·4	34·9 ± 2·9 (4)	52·1 ± 8·8 (4)	31·4 ± 0·2 (4)
Fungus comb	10·5 ± 7·0*	16·5 ± 2·6†	29·8 ± 4·0 (4)	9·9 ± 1·6 (4)	11·1 ± 0·3 (4)

*Uptake of O_2 from old comb.
†CO_2 emission at 28 °C.

$m^2\ s^{-1}$) was about two times higher than the emission of *O. pauperans* (28 nmol $m^2\ s^{-1}$). At the landscape-scale, the CO_2 flux due to *Odontotermes* (50 nmol $m^2\ s^{-1}$) was higher than that due to *A. cavithorax* (22 nmol $m^2\ s^{-1}$). In Lamto savanna, the total CO_2 flux due to the two termite species studied was thus 72 nmol $m^2\ s^{-1}$. Assuming a constant emission rate throughout the year, this corresponded to 2·28 mol $m^{-2}\ year^{-1}$, or 27·2 g C $m^{-2}\ year^{-1}$.

Discussion

COMPARISON OF MASS-SPECIFIC CO_2 PRODUCTION RATES AMONG TERMITE SPECIES

The mass-specific respiration rates obtained in this study are similar to those reported for other species of Macrotermitinae, whether from savanna or forest ecosystems (Table 5). The mean mass-specific respiration rate in *A. cavithorax* workers (72·8 nmol $mg^{-1}\ h^{-1}$) is close to that reported for *Macrotermes jeanneli* (77·3 nmol $mg^{-1}\ h^{-1}$) (Darlington *et al*. 1997), while the respiration rate of *Odontotermes* workers (129·6 nmol $mg^{-1}\ h^{-1}$) is close to that reported for minor workers of *Macrotermes bellicosus* (115·5 nmol $mg^{-1}\ h^{-1}$) (Collins 1977). The mean respiration rate of the soldiers of *A. cavithorax* (41·5 nmol $mg^{-1}\ h^{-1}$) and *Odontotermes n. pauperans* (52·1 nmol $mg^{-1}\ h^{-1}$) are intermediate between the respiration rates measured for *Macrotermes carbonarius* (25·3 nmol $mg^{-1}\ h^{-1}$) (McComie & Dhanarajan 1990) and *Macrotermes jeanneli* (57·4 nmol $mg^{-1}\ h^{-1}$) (Darlington *et al*. 1997). In these studies, the intercaste variation in respiration rates is generally correlated to the individual dry mass/fresh mass ratio and to the degree of sclerotization (Collins 1977). Soldiers with a high percentage of sclerotization exhibit low respiration rates compared with workers. Within each caste, minor individuals exhibit higher mass-specific respiration rates than larger individuals. The fungus comb respiration rates of the two species studied are closest to that reported for *Macrotermes bellicosus* (10·5 nmol $mg^{-1}\ h^{-1}$) (Collins 1977). Our respiration estimates for fungus-comb tissue were lower than those reported by McComie & Dhanarajan (1990) and Darlington *et al*. (1997), probably because our samples mixed new comb tissue with older parts that have a low respiration rate (Collins 1977).

To explain the measured differences in CO_2 emitted between *Ancistrotermes* and *Odontotermes*, one hypothesis is that the difference in respiration rates could be due to the difference in body size between the two species, as noticed by Sugimoto *et al*. (2000): smallest termites would produce greater amounts of CO_2 for the same biomass as the largest species. Firstly, if such a mechanism is operating, the expected result would be the opposite, as the *Ancistrotermes* workers are smaller than the *Odontotermes* workers (Table 2). Secondly, we found no correlation between the respiration rates and the termite individual weights. Rather such differences in respiration rates between species can probably be related to their digestive metabolism, as the rate of carbon dioxide production by different termite species represents a good estimation of their trophic status (Seiler *et al*. 1984; Brauman *et al*. 1992; Rouland *et al*. 1993; Jeeva *et al*. 1999). The Macrotermitinae species in which the workers exhibited higher respiration rates (e.g. *Macrotermes bellicosus* and *Odontotermes n. pauperans*) do ingest enzymes from the fungus, combined with their own enzymes for the digestion of their food (Rouland *et al*. 1991; Rouland 2000; Rouland & Bignell 2002), whereas other species exhibiting lower respiration rates for workers, such as *A. cavithorax*, do not.

COMPARISON BETWEEN FIELD AND LABORATORY MEASUREMENTS

Both field and laboratory measurements are needed for a reliable estimation of the impact of termite populations on gas emission (Khalil *et al*. 1990; Lawton *et al*. 1996; Sugimoto *et al*. 2000). Laboratory measurements can provide the determination of accurate respiration rates from isolated components of termite nests in standardized conditions. However, laboratory environmental conditions (low CO_2 concentration, few individuals, individuals under stress) are quite different from nest conditions. Furthermore, accurate estimates of the density of termite populations and fungus-comb chambers in the field are needed to extrapolate these laboratory estimates to the ecosystem scale. These two problems are of major importance if published data are to be used to assess the role of termites on CO_2 emission. Indeed, most of the termite studies in the literature concerned laboratory measurements (Breznak 1975; Zimmerman *et al*. 1982; Rasmussen & Khalil 1983; Darlington *et al*. 1997). Recent studies (Eggleton *et al*. 1999; Jeeva *et al*. 1999) utilized a Warburg manometer in the laboratory and measurements of methane fluxes from soil and mounds using static chambers. Some direct field measurements have been conducted (Seiler *et al*. 1984; Khalil *et al*. 1990), but very few studies have compared laboratory and field measurements (but see Fraser *et al*. 1986 on *Coptotermes lacteus*, for instance).

In most studies laboratory measurements were recorded to be much higher than field ones (e.g. Fraser *et al*. 1986; Khalil *et al*. 1990). In the present study, the results obtained from the two types of measurements were quite close. A similar result was obtained by Hébrant (1970) who found a good agreement between the respiration rate from whole *Cubitermes* nests and the sum of individual termite respiration in the laboratory. In our study of *Odontotermes n. pauperans*, estimates obtained in shrubby savanna were quite similar to laboratory estimates (Fig. 2), while estimates obtained in grassy and woody savannas were lower than laboratory estimates. The low values computed in grassy and woody savannas are probably minimum values, as a part of the CO_2 produced by a chamber may have leaked out of the sampled area. On the other hand, the relatively high value computed in shrubby savanna could be explained by the high density of fungus-comb chambers in this savanna type and by a possible effect of the surrounding fungus-comb chambers on the measurements that could partly compensate for the biases described above.

CONTRIBUTION OF FUNGUS-GROWING TERMITES TO CO_2 EMISSION FROM SOIL AT THE FUNGUS-COMB CHAMBER- AND MOUND-SCALES

Termite contributions to total soil respiration are due to direct CO_2 emissions from respiration by live tissues (termite and fungal tissues) and to indirect soil respiration due to the stimulation of soil microbial metabolism in the nest material. The soil respiration rate of termite fungus-comb chamber wall reported in our study was about seven times higher than for control soil in *Odontotermes n. pauperans* and five times higher in *Ancistrotermes cavithorax* (Table 1). These results are similar to those obtained by Abbadie & Lepage (1989) for *A. cavithorax* (four to five times higher). The respiration of the walls of fungus-comb chambers represents an heterotrophic activity, mainly microbial metabolism, and indicates the quantity of organic carbon mineralized by microflora (Legay & Schaefer 1981). Thus, at the point-scale, the direct respiration of termite individuals is accompanied by a priming effect of labile carbon sources enhancing soil organic matter mineralization. Our results showed that the majority of the CO_2 emitted from a fungus-comb chamber is produced by the fungus-comb itself. In their recent synthesis about the global impact of termites in the carbon cycle, Sugimoto *et al*. (2000) have underlined the very high rate of aerobic respiration from the fungus comb in Macrotermitinae.

The release of CO_2 by individual underground fungus-comb chambers leads to a high spatial heterogeneity of apparent soil respiration when measured at point scale, i.e. on 0·01 m^2 plots. Our estimates of CO_2 emission rates from control soil were similar to those obtained by Le Roux & Mordelet (1995) (5·2–10 $\mu mol\ m^{-2}\ s^{-1}$ vs. 6·6–9·6 $\mu mol\ m^{-2}\ s^{-1}$, respectively). Apparent soil respiration was two-fold higher when

measured above an underground fungus-comb chamber than where the chamber was absent. This result underlines the effect of termite nests on the heterogeneity of soil metabolism in a tropical savanna at a very fine (i.e. decimetric) scale, as stressed by Abbadie & Lepage (1989).

Termites also induce heterogeneity in CO_2 fluxes within a given savanna type at a scale of a few meters, because the CO_2 release from the two termite species studied was mostly concentrated on termite mounds. Indeed, according to data from Tables 2 and 3, total CO_2 emitted by termites ranged from 9·9 to 24·2 mol m^{-2} $year^{-1}$ (i.e. 118·8–290·4 g C m^{-2} $year^{-1}$) on termite mounds, compared with 0·6–2·3 mol m^{-2} $year^{-1}$ (i.e. 7·2–27·6 g C m^{-2} $year^{-1}$) in the surrounding soils.

CONTRIBUTION OF FUNGUS-GROWING TERMITES TO CO_2 EMISSION AT THE LANDSCAPE SCALE

At the landscape scale, and assuming a constant emission rate throughout the year, the CO_2 emitted by termites was around 1·58 mol m^{-2} $year^{-1}$ (or 18·9 g C m^{-2} $year^{-1}$) for *Odontotermes n. pauperans*, and 0·69 mol m^{-2} $year^{-1}$ (or 8·3 g C m^{-2} $year^{-1}$) for *Ancistrotermes cavithorax*. Josens (1972, 1974) estimated fungus-growing termite consumption in this ecosystem, from the turnover of the fungus-comb mass (Josens 1971), to vary between 1300 and 1600 kg ha^{-1} $year^{-1}$ (dry mass of litter). From the data given in Lepage *et al*. (1993), this amount included 41% of grass litter and 59% of tree litter and is equivalent on average to 645 kg C ha^{-1} $year^{-1}$ (64·5 g C m^{-2} $year^{-1}$). Thus, the respiration rates measured in this study represented roughly 42% of the carbon consumed by the Macrotermitinae populations. This value represents a sensible proportion, since the consumption estimated by Josens included other termite species (*Microtermes toumodiensis* and *Pseudacanthotermes militaris*) not studied in our work. Furthermore, a noticeable proportion of the carbon ingested is assimilated into termite biomass and dispersed, mostly by predation, or incorporated into termite structures (Jouquet *et al*. 2002), as galleries and soil sheetings, not taken into account in our study.

On the other hand, termite consumption represented 11·6% of the total above-ground primary production (herbaceous and woody species), estimated to be on average 558 g C m^{-2} $year^{-1}$ (from the figures given in Menaut & César 1979; balanced with the proportion of the savanna types as given in Table 4 and a carbon content of 43%). If we take into account the proportion of the above-ground production burnt by annual fires (57% in Menaut & César 1979), termite consumption amounted to 27% of the carbon in the above-ground primary production that was not mineralized by annual fires, a figure similar to the one given by Sugimoto *et al*. (2000) for savanna ecosystems.

Our results stress the importance of aerobic respiration from the termite food reserves, as the fungus-comb mass was responsible for 51% and 82% of the CO_2 flux emitted by chambers for *Odontotermes n. pauperans* and *Ancistrotermes cavithorax*, respectively. This conclusion is consistent with results of Wood & Sands (1978) and Seiler *et al*. (1984) who found that the *Termitomyces* fungus released the majority of the carbon ingested by the termites. This emphasizes the fact that the contribution of Macrotermitinae populations to CO_2 flux to the atmosphere is much greater than their biomass density data would suggest, as underlined by Sugimoto *et al*. (2000). This illustrates also the role of the fungus-comb in achieving C–N balance in termites, as outlined by Higashi *et al*. (1992): the release of C through fungus respiration being a way to concentrate nitrogen in the comb. Finally, our findings illustrated the necessity of taking into account respiration from the fungus-comb in assessing the role of Macrotermitinae in CO_2 emission at the landscape scale.

Conclusion

This study provides the first estimation of carbon dioxide fluxes from underground fungus-growing termites in the tropical humid savanna zone, based on laboratory-derived measurements of mass-specific respiration rates and field estimates of termite population density. Termite fungus-comb chamber respiration was shown to induce a high spatial heterogeneity in CO_2 evolution from soils when measured at the point scale (i.e. 0·01 m^2) and mound scale (a few m^2). At the landscape scale, the CO_2 emission rate due to the two underground fungus-growing termite species (around 27·2 g C m^{-2} $year^{-1}$) represented 42% of the carbon consumed by the termite populations and 11·3% of the carbon in the above-ground primary production not mineralized by annual fires.

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