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Ventilation and thermal constancy of a colony of a southern African Termite (*Odontotermes transvaalensis*: Macrotermitinae)

J. Scott Turner

Department of Biology, University of Bophuthatswana, Mmabatho, Bophuthatswana, South Africa

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Odontotermes transvaalensis is a subterranean macrotermitine common in the arid grasslands of north-western South Africa. These termites build a conspicuous above-ground chimney that meets the structural requirements of an induced-flow system for ventilating the colony. Pulses of tracer gas flow from ground-level entry holes into the colony and out the chimney. A pulse of tracer travels unidirectionally through the colony in an average of 19 min, with a time constant for clearance of tracer of, on average, 26 min. The clearance of tracer is affected by wind conditions in a way consistent with an induced flow mechanism, but other mechanisms, such as free convection within the colony, or forced ventilation by external winds, may play a minor and secondary role in translocating air within the colony. Obstructing ventilation of the colony does not have any discernible influence on colony temperature. It seems that ventilation of the *O. transvaalensis* colony does not play a significant role in the regulation of colony temperature.

Keywords: induced flow; termites; tracer methods; nests; ventilation

Introduction

Odontotermes transvaalensis is a fungus-growing macrotermite that is common in the thorn savannahs of the northern Cape Province and western Transvaal of South Africa (Ruelle, 1985). These termites are subterranean, with the active colony and its fungus gardens located as deep as 2 m below the surface of the ground (pers. obs.). However, a colony's presence is made conspicuous by a vertical hollow chimney that can rise as high as 2 m above the ground surface. The chimney tube opens into a large subterranean air space, the gallery, that is separated from the fungus gardens of the colony by a porous soil partition (Ruelle, 1985; Fig. 1). The chimney emerges from a low mound, denuded of vegetation and perforated by numerous small holes that provide openings to the colony below.

If one holds one's hand over the chimney opening, particularly on a cool night, one can feel a stream of warm air flowing out of it: this is not felt at any of the holes penetrating the surface of the mound (pers. obs.). It seems, therefore, that the remarkable above-ground edifice built by these termites plays some role in ventilating the colony.

Darlington (1987) has suggested that termites employ three basic strategies for

Address for correspondence: Department of Environmental and Forest Biology, College of Environmental Science and Forestry, State University of New York, Syracuse, NY 13210, U.S.A.

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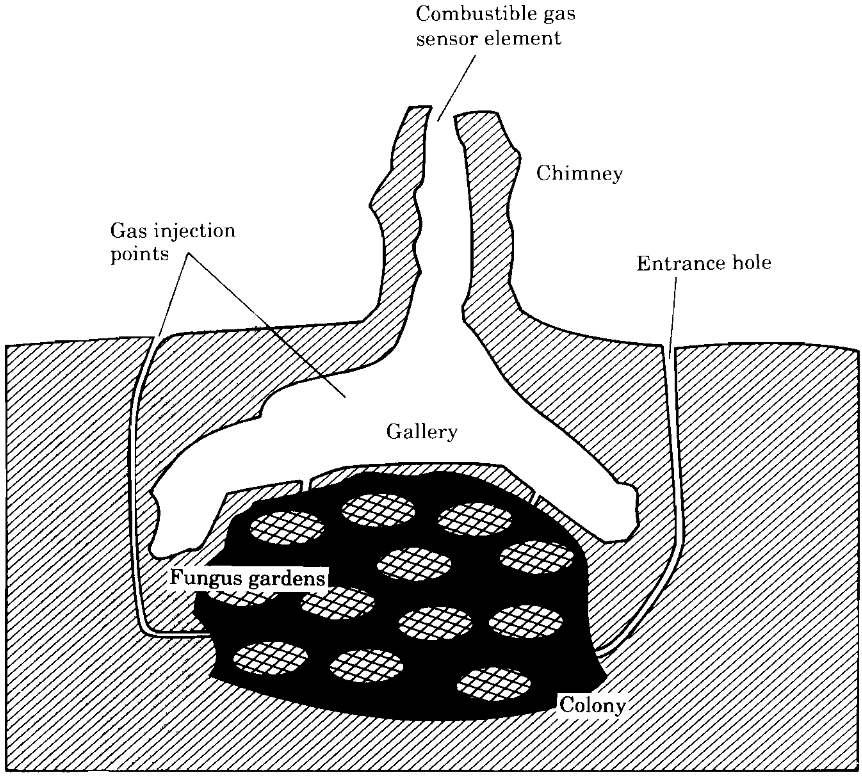

Figure 1. Schematic diagram of the colony of *Odontotermes transvaalensis*, based upon the description by Ruelle (1985), and on personal observations of excavated colonies. Location of in-line combustible gas sensor, and infection points for propane are indicated.

ventilating their enclosed colonies. One, typified by the completely enclosed colony of *Macrotermes bellicosus* (formerly *M. natalensis*), relies on free convection currents, set up in the colony by heat and water vapour production. These internally-driven air currents bring colony air to the porous walls of the colony's epigeous mound, where it exchanges respiratory gases, water vapour and heat with the outside. A second mechanism is exemplified by the colony of *Macrotermes subhyalinus*, which also is enclosed completely in an epigeous mound. In this case, the mound covering is perforated by holes. External winds blowing across the colony establish positive hydrostatic pressure gradients which force outside air through the colony. A third mechanism, typical of *Macrotermes jesmmeli*, employs a horizontal hole opened at the top of the epigeous mound. Air blowing tangentially across this hole draws colony air out through the hole by operation of a Venturi effect. External air is drawn into the colony through small holes in the base of the mound. Ventilation by a Venturi effect also has been claimed to operate in the epigeous colonies of *M. subhyalinus* (Weir, 1973).

The chimney and mound of *Odontotermes transvaalensis* fill the structural requirements for ventilation of the colony by a Venturi mechanism, known more generally as induced flow (Vogel, 1978, 1981). Ventilation by induced flow requires at least two openings to the structure to be ventilated: one raised off the surface of the ground, and one close to the surface. The variation of wind speed that naturally exists in a boundary layer means the two holes will experience different wind speeds. This will, in turn, induce a negative hydrostatic pressure difference between the two openings, such that air is drawn out the higher opening and into the lower opening. Whatever structure is interposed between the openings will thus be ventilated.

This paper explores two questions concerning the ventilation of an active colony of *O. transvaalensis*. First, I ask whether the ventilation of the colony plays any role in the regulation of its temperature. Second, I ask whether the colony is ventilated by induced flow or whether there are other mechanisms at work.

Materials and methods

Study site

The study was carried out on termite colonies inhabiting a tract of undisturbed vegetation, mostly grass with scattered thorn acacia scrub, on the campus of the University of Bophuthatswana, Mmabatho, Bophuthatswana, near Mafikeng, South Africa (25°53′S, 25°39′E). The topography of this region is flat, and the climate is warm and sunny: daytime maximum temperatures typically range from 25–35°C in summer to 15–25°C in winter. Rains usually come in summer thundershowers, and winters are commonly dry and clear.

Nearly all of the measurements reported here were done on a single active colony. The denuded mound associated with this colony was an oval measuring $0{\cdot}26 \times 0{\cdot}22$ m. The chimney was 0·94 m high, with an internal bore of roughly 10 cm.

Daily course of colony temperature

Daily courses of soil temperatures in and around an active colony were measured for a consecutive 9-day period beginning 9 May 1990. Measurements of temperatures were made using a data-logging system, consisting of a 16-channel multiplexed A/D converter (ADC-1, Remote Measurement Systems, Seattle, WA) driven by a field capable microcomputer (TRS Model 100, Tandy Corp, Dallas, TX).

Temperatures at 14 locations in and around the colony were measured. Four sets of three (= 12) 16 Ga thermocouples (type K) measured temperatures at three vertical locations in the soil: at the surface (0 cm), at −20 cm and at −50 cm. The thermocouples were positioned by wiring them to a metal stake, one at the bottom, one 30 cm from the bottom and one 50 cm from the bottom. The stake was then driven 50 cm into the ground. Stakes with attached thermocouples were driven at four locations: Site 1 (at the centre of the mound), Site 2 (at the periphery of the mound), Site 3 (at vegetated ground 4 m from the periphery of the mound), and Site 4 (at the centre of an abandoned and inactive mound 8 m from the active mound). I had previously determined with a metal probe that −50 cm at site 1 would have located the thermocouple in the fungus gardens of the colony. It was discovered at the end of the study that the deep thermocouple at site 4 (the inactive mound) had slipped to a depth of −35 cm while the stake was being driven in. One additional thermocouple (24 Ga) was placed into the chimney of the active mound to measure chimney air temperature. Finally, one thermocouple was wired to a stake to measure air temperature at +60 cm above the active mound.

Meteorological conditions at the study site

Prevailing meteorological conditions during the study were measured at two sites in the vicinity of the colony. A student weather station maintained at the University of Bophuthatswana campus provided once-daily readings, taken at 1400 h, of air temperature, soil temperature at various depths, relative humidity, wind speed and wind direction. Continuous records of air temperature and humidity were obtained from a weather station maintained at the Mmabatho International Airport by the South African Weather Service (Station 0508047 0), roughly 6 km NW of the study site. These readings showed high correspondence with the once-daily readings from the university weather station (for air temperature, $r^2 > 95\%$: for relative humidity, $r^2 > 86\%$), and so were assumed to reflect conditions at the study site.

Altering air flow through the colony and daily course of colony temperature

While the soil temperatures described above were being measured, the flow of air at the chimney was modified in various ways. During the first three days, designated Control period 1, the colony was left undisturbed. On days 4–5, designated 'Capped', an air-tight plastic covering was placed over the chimney mouth to block any air flowing out of it. On days 6–7, designated Control period 2, the plastic covering was removed, leaving the colony undisturbed again. Finally, on days 8–9, designated 'Breached', a 4 cm hole in the base of the chimney wall was opened and kept open.

Flow of tracer gases through the colony

The flow of air through the colony was evaluated by measuring the appearance in the chimney of a pulse of propane tracer gas introduced into the colony. The tracer gas was introduced via a hose attached to a portable propane cylinder, fitted with a 23 psi step-down regulator. The propane tracer gas was detected by a field-capable instrument that used a solid state combustible gas sensor, sensitive to <1 p.p.t. propane in air (TGS-813, Figaro U.S.A., Wilmette, IL). The sensor, with a compensating thermistor, was fitted into a 10 cm length of PVC pipe (Fig. 2). This assembly formed an inline combustible gas sensor (ICGS) that fitted into the chimney and sensed the presence of tracer gas in the chimney without blocking the flow of air through the chimney (Fig. 2). When the ICGS was in place, the sensor itself was located about 8 cm down from the chimney rim (Fig. 2). The ICGS and associated signal conditioning instrumentation was powered by a 12V rechargeable lead-acid battery (2A–h), which could operate the device continuously for about 7 h.

The sensor was calibrated by exposing it to known concentrations of propane gas in air. The calibration chamber was constructed from a 1 m length of polyvinyl chloride pipe. The ICGS could be fitted to one end of the pipe and capped to form one sealed end. The other end of the pipe also was sealed with a PVC cap. Volume of the chamber was calculated from the internal dimensions of the pipe. Known volumes of 100% propane were added to the chamber with a syringe, and the equilibrium reading of the sensor was determined. Typical concentrations of propane in this experiment were 1–10 p.p.t. propane.

A variety of tracer experiments were carried out, but all followed a standard protocol: the sensor was first allowed to equilibrate in fresh air and the instrument was calibrated to zero. The ICGS was then fitted into the chimney, and readings were taken for a 5 min pre-sampling period to establish a baseline reading. A 5 s pulse of propane was then introduced, this time being designated as time 0. Readings from the sensor were taken every 30 s, and usually carried on until tracer gas levels in the chimney had returned to within 20% of initial readings. The sensor was then removed from the chimney and allowed to re-equilibrate in fresh air. The last step was to check and correct for drift in the sensor.

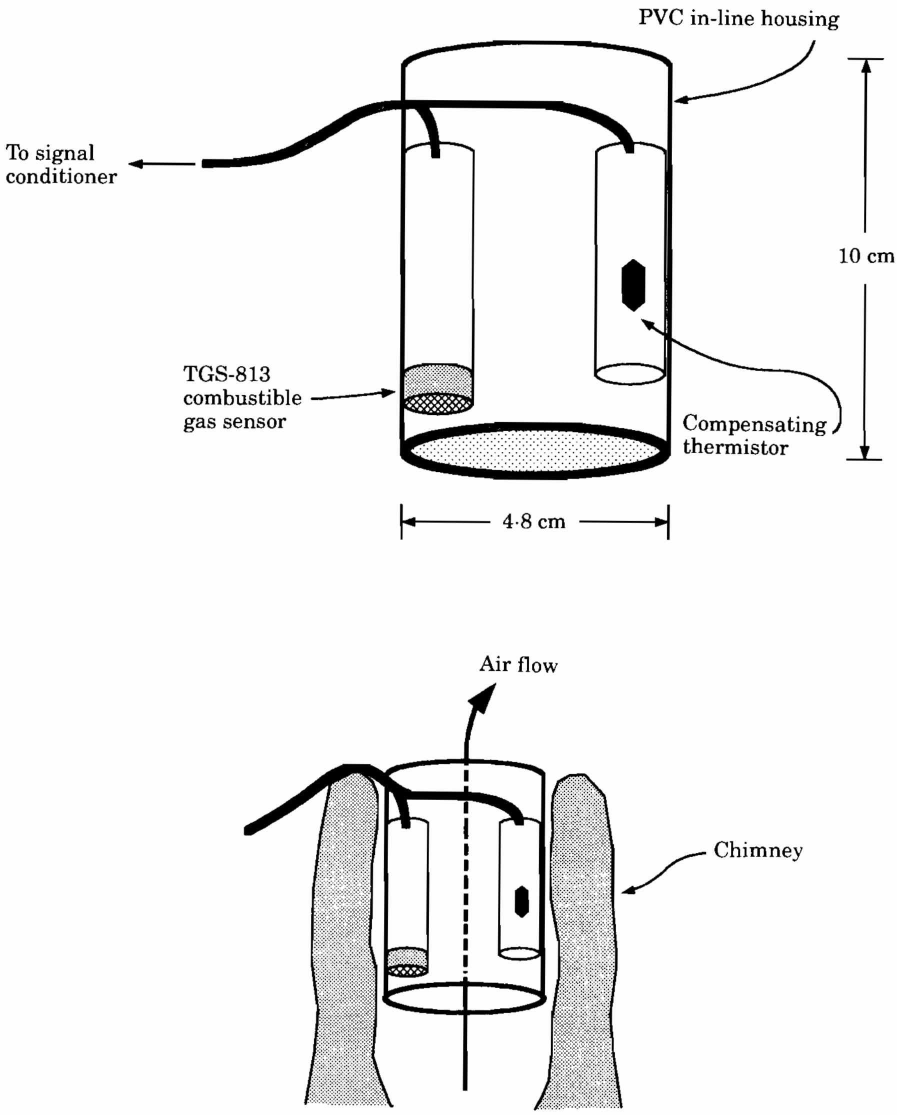

Figure 2. Schematic diagram of inline combustible gas sensor (ICGS) and its typical placement in the chimney of an *Odontotermes transvaalensis* colony.

Evaluation of tracer clearance rates

The time course of tracer concentration at the chimney usually showed the pattern typical of a tracer pulse experiment (Sheppard, 1962; Welch *et al.*, 1972): i.e. an increase in tracer concentration beginning at some time after introduction of the gas, rising to a peak value, and followed by an exponential washout of the remaining tracer. To quantify the clearance of the tracer, two numbers were calculated from the tracer concentration data. The time at which the peak occurred, designated t_{max}, represents the modal time of travel of the tracer molecules from the point of introduction to the point of egress. The time constant for the exponential washout curve, designated τ, represents the time required for 63% of the tracer to clear, and so is proportional to the residence time of gas in the colony. As a rule of thumb, roughly 95% of the air in the colony is exchanged with the environment in a period of roughly 3τ.

The peak time, t_{max}, was calculated by first fitting a 3rd order plynomial equation to the data around the peak. This polynomial was then differentiated and the root of the differential (equivalent to the elapsed time from introduction of tracer to the appearance of the peak) was estimated. The time constant was calculated by estimating the slope of the post-peak graph of ln ($[T_t]/[T_0]$) vs. time, where $[T_{0,t}]$ is the concentration of tracer at times 0 and t, respectively. The time constant is the negative inverse of this slope.

Effect of wind conditions on tracer clearance

The effects of prevailing wind conditions on tracer clearance were assessed in three ways. Qualitative notes of the wind conditions were made at the times of the various tracer experiments, classifying the prevailing conditions as calm, steady breeze or gusty, as well as noting the wind direction. In addition, wind conditions at the chimney were experimentally altered in two ways and the effects on tracer clearance observed. To eliminate breezes at the chimney without altering the exchange of air between the chimney mouth and the outside air, a loose-fitting box was placed over the top of the chimney. In another experiment, a windbreak that could be quickly raised or lowered was erected in front of the chimney. Tracer concentrations when the windbreak was up were then compared against those when the windbreak was down.

Clearance of tracer at different times of day

From 27 October 1992 to 7 November 1992, several tracer pulse experiments were carried out to compare clearance rates during the day (1100 h) with those at night (2200 h).

Results

Weather conditions during 9–17 May 1990

Weather conditions during the period 9–17 May are summarized in Fig. 3. A cold front passed over the Mmabatho area during Control period 1, with attendant cloudy conditions, low daily amplitude of air temperature, high humidities (Fig. 3) and a moderating of soil temperatures (Table 1). Six millimetres of rain fell on 11 May. For the other experimental periods, generally sunny conditions prevailed, and weather conditions for the experimental periods covering 12–17 May were roughly similar (Fig. 3).

Colony temperatures during periods of altered air flow through the chimney

At a depth of − 50 cm, soils at site 1 (the active colony) were on average 2–3°C warmer than temperatures at any of the other sites (Table 1). Comparing the experimental periods, soil temperatures at all measured sites were evidently moderated during Control period 1 (Table 1), presumably as a result of the colder weather and lack of insolation during this period (Fig. 2). However, comparing the colony temperatures during the experimental periods, where the chimney was capped or breached, with the meteorologically similar conditions that prevailed during Control period 2, showed that average temperatures

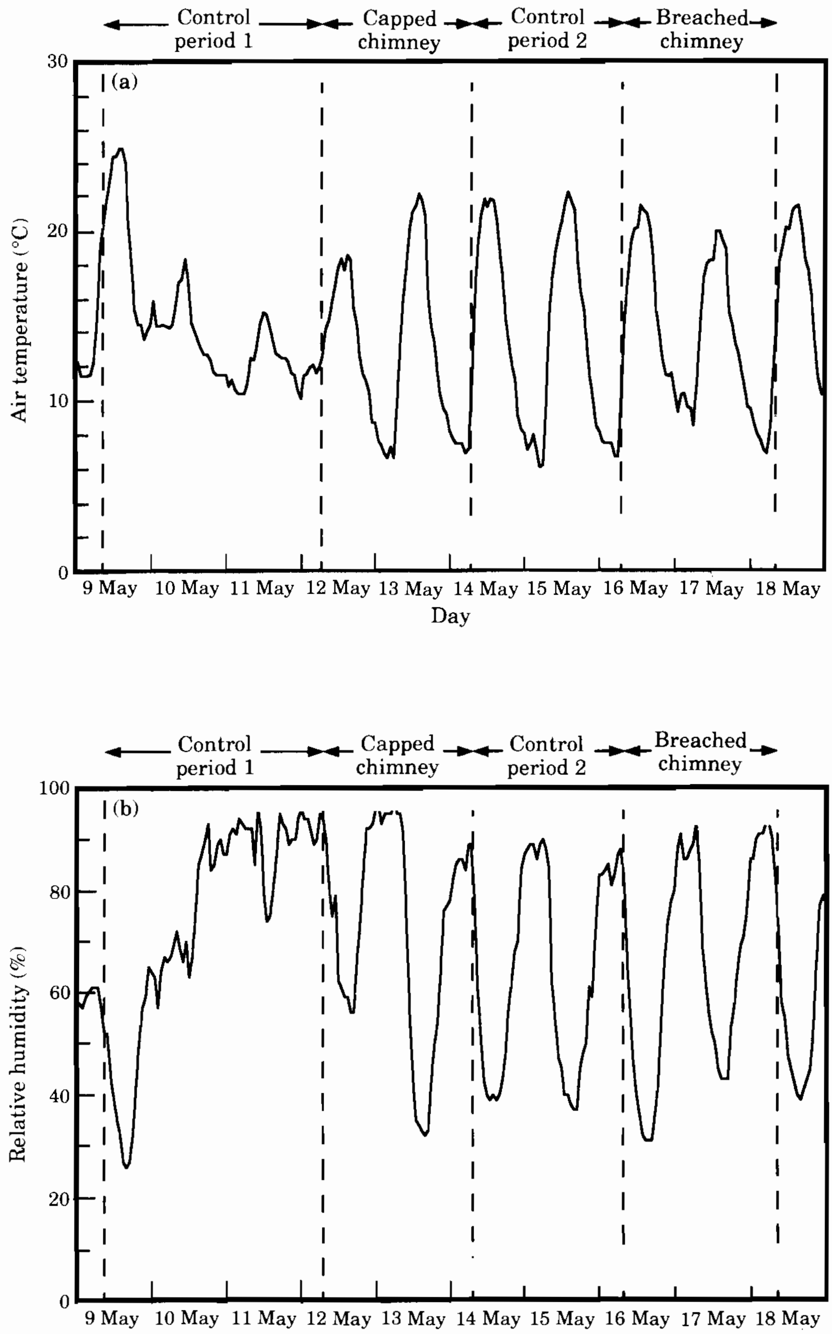

Figure 3. Weather conditions at the Mmabatho International Airport (roughly 6 km NW of the location of the termite mount) for the days 9–18 May 1990. (a): hourly variation of air temperature. (b): hourly variation of relative humidity.

Table 1. *Soil temperatures at −50 cm in and around an active* Odontotermes transvaalensis *colony during the experimental periods described in the text. Numbers are mean (maximum–minimum) temperatures for the periods indicated. Average soil temperatures at −60 cm for these periods are also reported for the weather station located at the University of Bophuthatswana*

	Control period 1 (9–11 May)	Capped chimney (12–13 May)	Control period 2 (14–15 May)	Breached chimney (16–18 May)
Active colony	21·5	20·8	21·0	20·9
(Site 1)	(22·3–20·0)	(21·8–19·5)	(21·8–19·7)	(21·6–19·9)
Colony periphery	19·0	18·1	18·2	18·2
(Site 2)	(20·6–17·4)	(19·1–16·4)	(19·2–16·9)	(19·2–17·2)
Vegetated ground	18·1	17·7	17·7	17·6
(Site 3)	(18·9–17·1)	(18·9–16·4)	(19·0–16·5)	(19·1–16·5)
Inactive mound	17·8	17·7	17·8	17·8
−35 cm (Site 4)	(20·2–15·6)	(20·5–14·8)	(20·6–14·4)	(20·2–15·1)
Weather station	19·1	18·3	18·3	18·3
−60 cm (University)				

between the periods varied by no more than 0·2°C (Table 1), indicating no apparent influence of chimney air flow on colony temperature (Table 1).

Excurrent air temperatures during periods of altered air flow through the chimney

Temperature of the chimney air covaried in a complex way with the temperature of the abmient air, particularly during the daylight hours (Fig. 4). Comparing the temperatures during Control period 1 (when there was little insulation) with those during Control period 2 (when insulation was greater) suggests that solar heating of the chimney and ambient air was the principal source of this covariation (Fig. 4). During the cloudy conditions that prevailed during Control period 1, chimney air temperature was consistently 5–6°C warmer than the ambient air (Figs 4, 5; Table 2). During the sunny conditions that prevailed during Control period 2, a very different picture is evident (Fig. 4). During the night-time hours, chimney air temperature is 10–12°C warmer than ambient air temperature (Fig. 4). Shortly after sunrise, ambient air temperature increased quickly, so that by 0900–1000 h, chimney air temperature was slightly cooler than the ambient air temperature (Fig. 4). By roughly 1300 h, chimney air temperature again exceeded ambient temperature (Fig. 4). Presumably, solar heating of the chimney walls during the day, and a greater cooling of ambient air at night were responsible for the complex covariation of temperature of the chimney air and ambient air.

To assess the effect of altering airflow through the chimney, statistical comparisons were made for the night-time hours of 2200 h to 0200 h, when the complex temperature covariations evident during the day were absent. Night-time air temperatures were warmest during Control period 1, reflecting a moderating influence of cloud cover on those nights (Table 2). Night-time air temperature during the other, less overcast periods were significantly cooler (Table 2). During Control periods 1 and 2, when the chimney was left uncapped, chimney air temperature averaged 16·9 and 17·4°C, respectively, and did not differ significantly from one another (Table 2). Upon capping the chimney, chimney air temperature fell to about 12·4°C, or 5·0°C warmer than ambient air temperature (Table 2). When the chimney was breached, chimney air temperature fell to roughly 10·7°C, only 2·5°C warmer than air temperature (Fig. 5; Table 2).

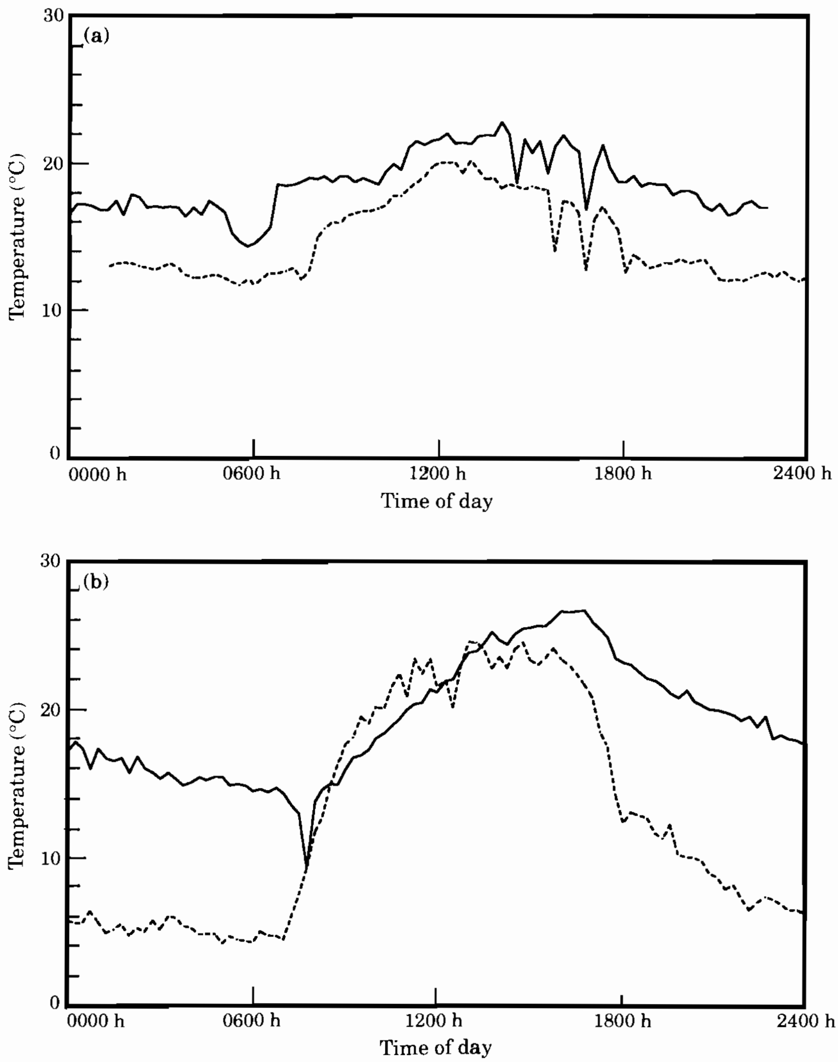

Figure 4. Daily average course of temperature of chimney air (solid line) and ambient air at 60 cm above the ground (dotted line) for the experimental periods indicated in the text. (a) control period 1. (b): control period 2.

Tracer clearance times for unobstructed chimneys

For tracer pulses introduced with no obstruction at the chimney, t_{max} averaged 19 min, and ranged from about 10–33 min (Table 3). The clearance time constants for these measurements averaged roughly 26 min, and ranged from 12–40 min (Table 3).

Patterns of gas flow through a colony

Several measurements of propane clearance were carried out on 17 August on a colony that had three chimneys. The sensor was placed into a chimney that had active termites

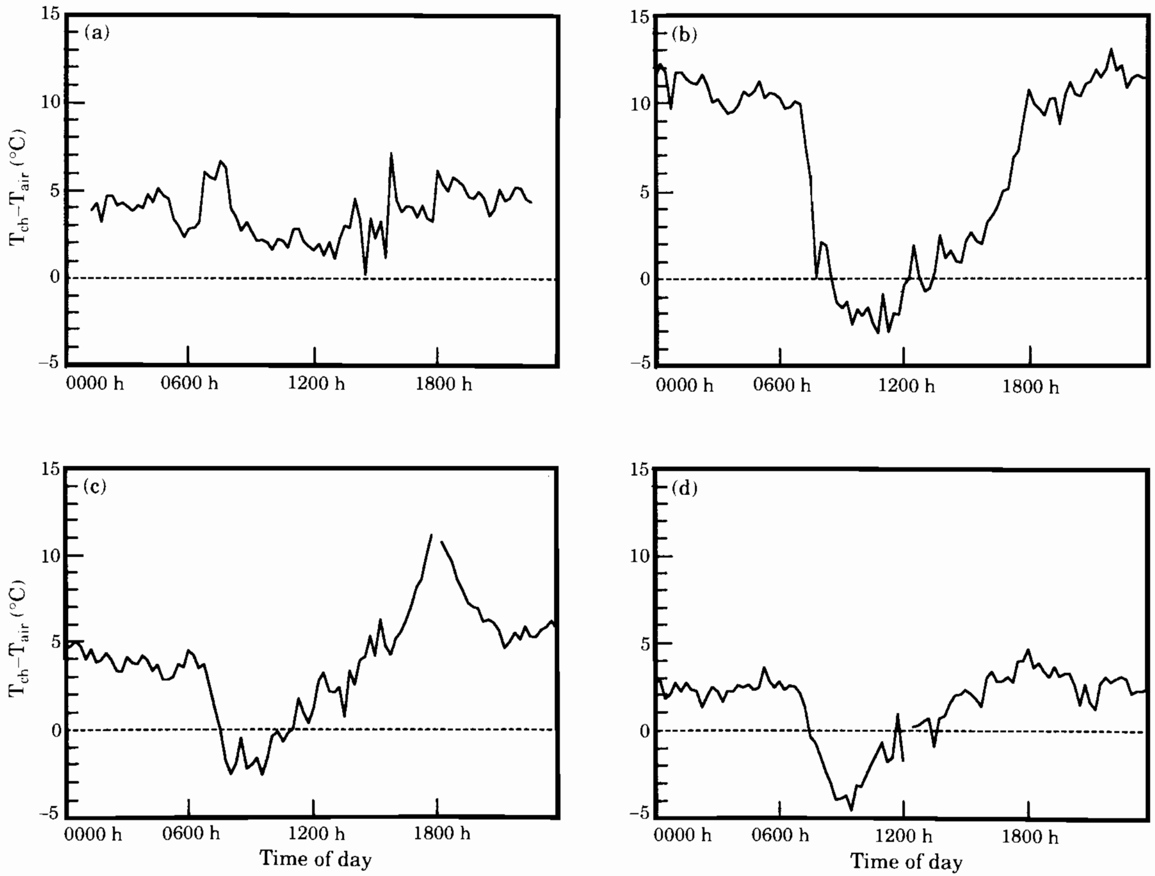

Figure 5. Daily average course of the temperature difference between chimney air (T_{cn}) and ambient air at 60 cm above the ground (T_{air}). (a): control period 1. (b): control period 2. (c): chimney capped. (d): chimney breached.

Table 2. *Comparisons of chimney air and external air temperatures for the night-time hours 2200–0200 h. Numbers represent mean values with least significant ranges in brackets, calculated at* p = *0·05*

Period	Chimney temperature (°C)]	External air temperature +60 cm (°C)	Chimney–external air temperature (°C)
Control period 1	16·90	12·65	4·25
	(17·08–17·80)	(12·34–12·96)	(3·93–2·57)
Capped chimney	12·42	7·39	5·04
	(12·06–12·78)	(7·08–7·70)	(4·72–5·36)
Control period 2	17·44	6·09	11·35
	(16·54–17·26)	(5·78–6·40)	(11·03–11·67)
Breached chimney	10·68	8·16	2·52
	(10·32–11·04)	(7·85–8·47)	(2·20–2·84)

Table 3. *Peak times* (t_{max}) *and time constants* (τ) *for clearance of tracer gas from colonies with unobstructed chimneys*

	t_{max} (min)	τ (min)
Mean	18·6	26·4
S.D.	7·1	8·3
Maximum	32·7	40·4
Minimum	9·7	11·9
n	13	11

(designated the active chimney), and tracer gas was injected into various openings to the colony: once, into a surface entrance hole, once by snaking the gas hose through the active chimney into the gallery and introducing the gas there, and once into a chimney that appeared to be inactive, so judged because no worker termites were evident in it and spiders had established webs across the chimney mouth.

When gas was introduced into the gallery, tracer appeared almost immediately at the chimney ($t_{max} = 1{\cdot}6$ min), and was completely cleared by 6 min (Fig. 6). When a pulse of tracer gas was introduced into the vent hole, it appeared at the chimney later ($t_{max} = 6$ min), and required more than 30 min to clear (Fig. 6). Gas introduced into the inactive chimney never appeared at the active chimney: either the inactive chimney had been sealed off from the colony, or there was no net flow of air from one chimney to another.

Effect of wind on clearance of tracer gas

Wind appeared to affect clearance of tracer from the colony, albeit in a varied and complex way. If the air was very still, tracer concentrations in the chimney would at times first increase and then stay high (Fig. 7(a)). If breezes were moderate and steady, the tracer concentration would show the typical course of a tracer pulse experiment (Fig. 7(b)). During some measurements carried out when winds were gusty, a clearance curve would

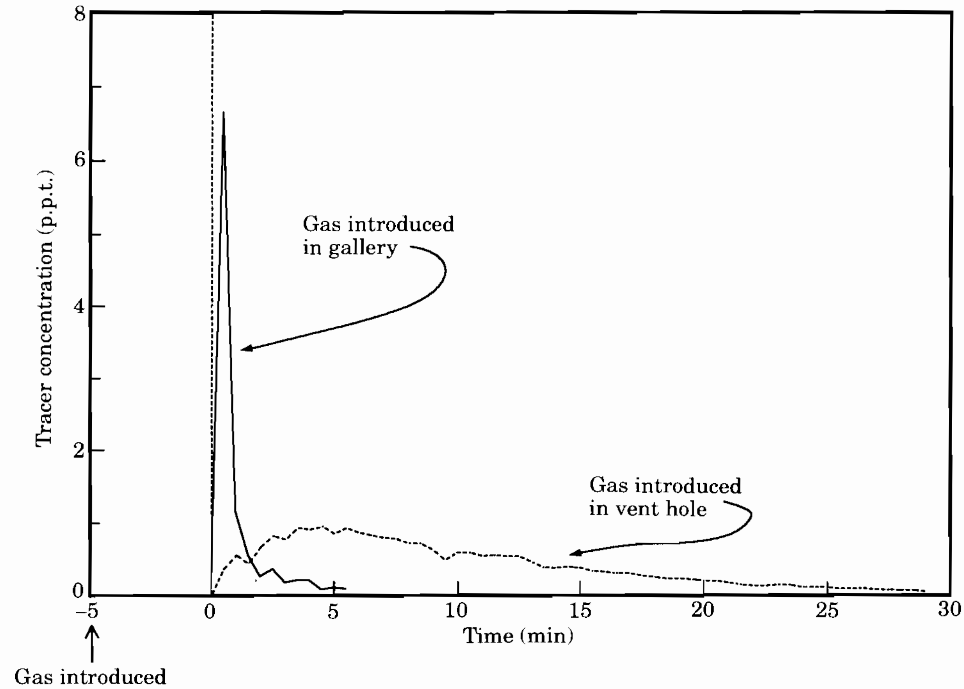

Figure 6. Clearances of tracer gas (propane) from an *O. transvaalensis* colony with multiple chimneys (17 August 1990). Details of experiment described in text.

be evident, but punctuated with abrupt drops in tracer concentration (Fig. 7(c)). Under particularly gusty conditions, even a clearance curve would not be evident. Rather, the tracer would occasionally appear in the chimney for brief periods and then as abruptly disappear (Fig. 7(d)).

Compared to clearances of tracer gas when the chimney was unobstructed (Table 3), capping the chimney with a loose-fitting box increased the peak time, t_{max}, by roughly 40% (Tables 3, 4), and increased the time constant for tracer clearance, τ, by roughly 60% (Tables 3, 4). A *t*-test showed both differences to be statistically significant: for t_{max}, $p = 0{\cdot}027$, and for τ, $p = 0{\cdot}023$.

Table 4. *Peak times* (t_{max}) *and time constants* (τ) *for clearance of tracer gas from colonies with chimneys capped with a loose fitting box*

	t_{max} (min)	τ (min)
Mean	25·6	42·1
S.D.	6·1	13·3
Maximum	35·5	55·9
Minimum	18·1	20·2
n	5	4

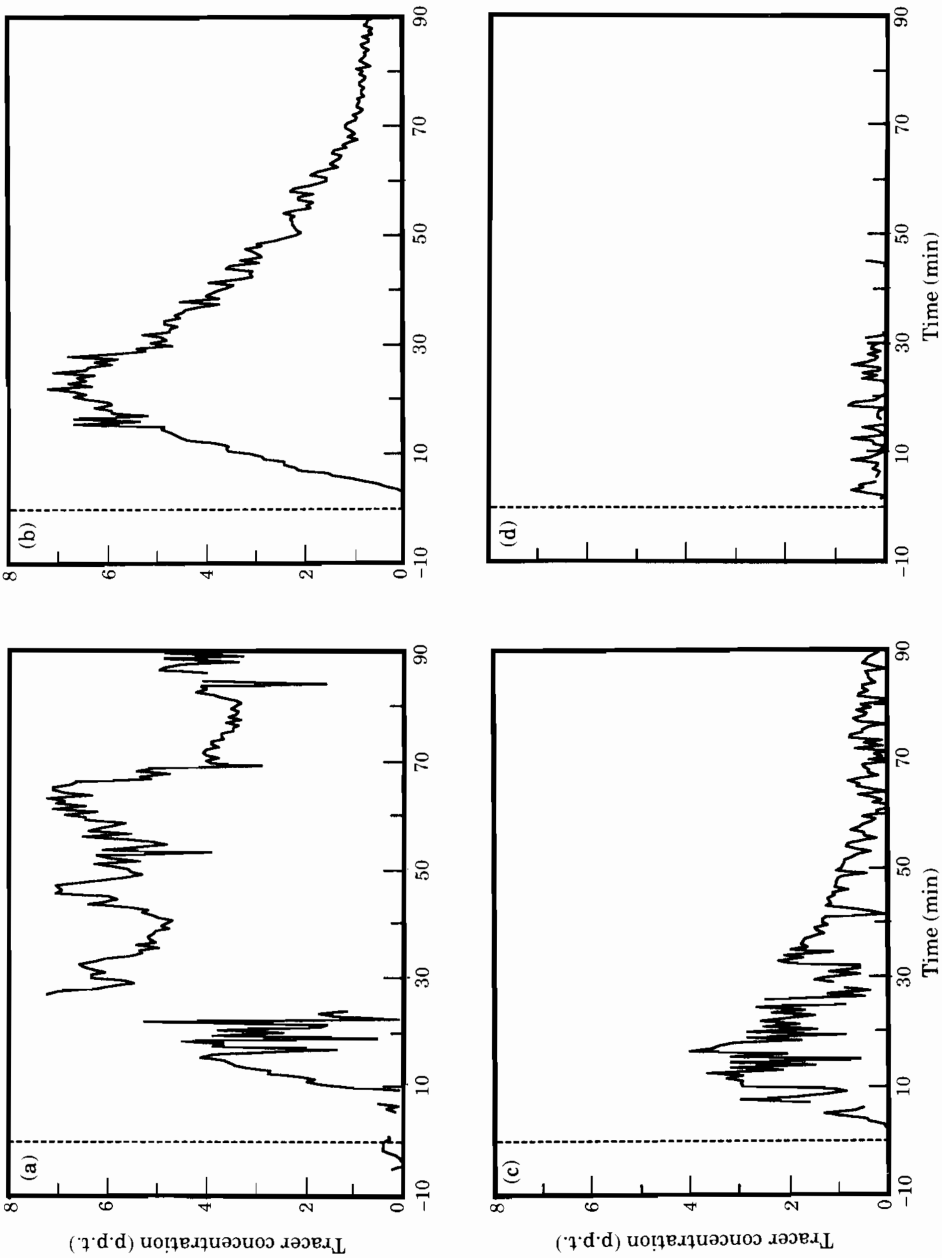

Figure 7. Representative clearance curves obtained for an *O. transvaalensis* colony during various wind conditions. (a): tracer concentrations at chimney during still air conditions (27 September 1990, 1540 h). (b): tracer concentrations at chimney during a steady moderate breeze (29 October 1990, 2215 h). (c): tracer concentrations at chimney during moderate gusty winds (1 September 1990, 1350 h). (d): tracer concentrations at chimney during heavy gusty winds (24 August 1990, 1430 h).

Table 5. *Effect of erecting a windbreak on concentration of propane tracer gas (in p.p.t.) in the chimney of an* O. transvaalensis *colony subsequent to introduction of tracer gas into a surface vent hole*

	Mean	S.D.	*n*
Windbreak erected	8·22	0·12	16
Windbreak down	0·49	0·05	18

Alternately erecting and lowering a windbreak in front of the chimney caused large variations in the concentration of tracer gas at the chimney. When the windbreak was present, and the chimney sheltered from the wind, the concentrations of propane tracer were roughly 17 times higher than when the windbreak was down (Table 5).

Clearance of tracer at different times of day

The peak time, t_{max}, for a propane tracer pulse was slightly faster during the day than during the night (Table 6). A *t*-test showed this difference to not be statistically significant ($p = 0{\cdot}200$). The time constant for clearance, τ, was slightly slower during the day than during the night (Table 6). This difference also was not statistically significant ($p = 0{\cdot}375$).

Discussion

Social insect colonies usually are ventilated in some way, so that environmental conditions inside the colonies can be maintained and regulated (Scherba, 1957; Lüscher, 1961; Stuart, 1972; Seeley, 1974; Grigg & Underwood, 1977; Seeley & Heinrich, 1981; Darlington, 1987; Nicolas & Sillans, 1989). The mechanics of colony ventilation are reasonably well understood for certain social insects like honeybees, which can heat their wings in place at the hive entrance to force air through the hive (Lindauer, 1961; Seeley, 1974; Southwick & Moritz, 1988).

Ventilation of the colony is not so well understood for flightless social insects like termites and ants (Noirot, 1970; Wilson, 1971; Hölldobler & Wilson, 1990), which, of course, have no wings to force air through the colony. In these insects, three ventilatory mechanisms probably are important (Darlington, 1987): (a) the 'thermosiphon', which relies on free convection currents within the colony, arising through gravity acting on local

Table 6. *Time of day and clearance of a pulse of propane tracer gas measured at the chimney of an* O. transvaalensis *colony*

	t_{max} (min)		τ (min)	
	1100 h	2200 h	1100 h	2200 h
Mean	14·1	17·6	25·3	23·2
S.D.	5·8	3·4	9·5	5·9
Maximum	22·3	21·6	32·6	30·5
Minimum	9·7	12·1	11·9	14·6
n	3	3	4	4

density variations of colony air (Ruelle, 1964; Cönen-Staß *et al.*, 1980); (b) positive forced ventilation, in which wind forces air through a porous epigeous mound; and (c) induced flow, where a Venturi mechanism draws air through the colony (Weir, 1973; Vogel, 1978, 1981).

The mound and chimney of *Odontotermes transvaalensis* conform to the structural requirements for ventilation by induced flow. The experiments reported here provide three additional lines of functional evidence that bolster the conclusion that the colony is ventilated by induced flow.

First, there is a clear directionality to air flow through the colony, and this direction conforms to that predicted for an induced flow system. Air emerges from the chimney, as evidenced by the excurrent stream of warm air from the chimney that one can feel with the hand (pers. obs.). A tracer gas that is introduced into the surface entrance hole eventually appears in the chimney, on average in about 19 min (Table 2). Finally, tracer introduced into the gallery below the chimney appears in the chimney in about one-fifth of the time required for tracer introduced into a surface entrance hole to appear (Fig. 5). Clearly, the net direction of air flow in these colonies is typically: surface entrance hole→gallery→ chimney.

Second, reducing wind speed past the chimney mouth slows the clearance of tracer from the colony, as expected for an induced flow system. Time to peak tracer concentration, t_{max}, and the time constant for tracer clearance, τ, both were lengthened by 40–60% when the top of the chimney was covered by a loose-fitting covering (Tables 3, 4).

Third, 'short-circuiting' air flow through the chimney, by breaching a hole at its base, appears to draw cooler ambient air directly into the chimney, rather than through the warmer colony. When the chimney is breached, there is a close correspondence between temperatures of the chimney air and outside air temperature, in marked contrast to the more elevated chimney air temperatures seen when the chimney is intact and unobstructed (Table 2). Thus, there is apparently a negative hydrostatic pressure gradient between the surface of the mound and the chimney mouth (Figs 4, 5; Table 2).

While these lines of evidence indicate that the *O. transvaalensis* colony is ventilated by induced flow, other results suggest that the colony could also be ventilated by other means. For example, in induced flow ventilation, absence of wind should retard clearance of tracer from the colony. For an uncovered chimney, this was the observed result when prevailing winds were still (Fig. 7(a)). Reducing air flow past the chimney mouth by covering it with a loose-fitting box gave a similar result (Table 4). However, in gusty winds, tracer was sometimes observed to abruptly disappear from the chimney mouth (Figs 7(c, d)). This disappearance of tracer can only mean that fresh outside air is being forced down into the chimney rather than tracer-laden colony air being drawn out of it. In some trials, this reversal of flow was an occasional event (Fig. 7(c)): in other trials, where the tracer only appeared occasionally in the chimney (Fig. 7(d)). the predominant direction of air flow was down the chimney.

This reversal of air flow through the chimney probably is caused by the chimney mouth occasionally acting as a wind 'scoop', rather than as the Venturi orifice required for induced flow to operate. The chimney is continually changing shape, through erosion by wind and rain, and the building activities of the colony's inhabitats – one colony I observed increased the height of its chimney by 80 cm in 3 months (pers. obs.). Consequently, as the chimney is extended, the plane of the orifice at the chimney mouth is often at some angle to the horizontal. Often, the termites build complex shelves and projections from the chimney mouth preparatory to extending its height (pers. obs.). It is easy to see how a chimney mouth that was not horizontal might act as a wind 'scoop' if wind flowed in one direction, but as an induced flow system if the wind flowed in the other (Weir, 1985). Air flow through the chimney also might be reversed by turbulence in the wind blowing around the chimney. The net vector of wind direction in a turbulent boundary layer often departs from the horizontal (Campbell, 1977), and if the wind vector occasionally pointed down rather than horizontal, outside air would then be forced into the chimney mouth.

Normally, air being forced through a system by forced convection would be expected to reduce the importance of air movements by free convection. If forced convection is an important mechanism for ventilating the *O. transvaalensis* colony, does this obviate any role for free convection in colony ventilation?

My observations suggest that air movements by free convection might occur within the colony, but that these probably play a secondary role in colony ventilation. For example, the active colony of *O. transvaalensis* is separated from the subterranean gallery by a porous barrier (Ruelle, 1985). Air that is heated and humidified in the fungus combs could therefore circulate in a convection cell from the bottom of the subterranean colony to the top, where it could exchange heat and water vapour with the gallery air by diffusion through the porous barrier. This is similar to the exchange that occurs across the walls of the epigeous mound of *M. bellicosus* (Lüscher, 1961; Ruelle, 1964). If the gallery air is humidified and heated by this exchange, this could set up a secondary convection cell in the gallery, moving warm and humid air up to and out the chimney. This mechanism is thought to operate in colonies of the macrotermite genus *Protermes*, which also build above-ground chimneys (Grassé & Noirot, 1958; Seeley & Heinrich, 1981).

If this is occurring, one should see the appearance of tracer at the chimney, even in the absence of any wind, particularly for a tracer like propane that is heavier than air. Three observations suggest that such a passive translocation of gas into the chimney does occur in the *O. transvaalensis* colony, even in the absence of any forced movement of air.

First, when the chimney is capped by an airtight plastic covering, the air in the chimney has certain characteristics of colony air. In the capped chimney, air is 4–5°C warmer than the surrounding air, even during the night when the chimney air temperature is not complicated by solar heating of the chimney wall (Fig. 5; Table 2). This temperature elevation is similar to that seen during the cloudy and moderate conditions of Control period 1 (Fig. 5; Table 2), when flow of air into the chimney from below was unrestricted. The air in the capped chimney is also very humid, as evidenced by a considerable condensation that appeared on the inside surface of the plastic film used to cap the chimney (pers. obs.).

Second, when prevailing wind conditions were still, tracer gas introduced into a surface hole could still be detected at the chimney, albeit very slowly and irregularly (Fig. 7(a)). Similar results were evident when wind speed at the chimney mouth was experimentally reduced by covering the chimney with a loose-fitting box (Table 4). Thus, even in still air conditions, there is apparently a net movement of gas from the surface holes to the chimney. Had there not been such a flow, tracer would have escaped out the surface holes and probably not been detected.

Third, when the prevailing wind conditions were acting to drive fresh air into the chimney mouth, experimentally reducing the wind speed at the chimney mouth with a windbreak actually resulted in an increase of tracer concentration at the chimney mouth (Table 5). The appearance of the tracer when the windbreak was erected could only have happened if tracer-laden air from deeper in the colony had drifted passively into the chimney.

Whatever role free convection plays in ventilating *O. transvaalensis* colonies, it appears that it is secondary to induced flow. For example, if free convection dominated gas exchange, one would predict that tracer clearance would be faster at night, when the density gradients arising from temperature and vapour density differences with the outside air are greatest (Fig. 5). This was not found to be the case: no significant differences between night and day values of either t_{max} or τ were evident (Table 6).

Ventilation of social insect colonies, however accomplished, is thought to help regulate colony gas exchange or colony temperature (Lindauer, 1961; Lüscher, 1961; Wilson, 1971; Weir, 1973; Seeley, 1974; Grigg & Underwood, 1977; Darlington, 1987; Southwick & Moritz, 1988). It appears that ventilation of *O. transvaalensis* colonies does not play a role in temperature regulation of the colony. This is in contrast to the African termite *Macrotermes subhyalinus*, which also has an induced flow ventilation system (Wier, 1973).

In the *M. subhyalinus* colony, capping the chimney mouth of the colony causes colony temperature to increase by nearly 10°C (Wier, 1973), probably because evaporative cooling of the colony has been obviated. No such temperature elevation was evident when the chimney mouth of an *O. transvaalensis* colony was capped, or when flow through the colony was 'short-circuited' by breaching a hole in the base of the chimney (Table 1). It is probable that ventilation is more important for the colony's gas exchange than for regulation of its temperature. Thermal stability is probably provided by the termites locating the colony deep underground: save for the 2–3°C elevation of colony temperature caused by the metabolic heating of the mound, the temperature fluctuations in the colony are identical to those found at similar depths of uninhabited soil (Table 1).

In summary, the southern African termite, *Odontotermes transvaalensis* locates its colony deep underground. Although the metabolic activity of the colony warms it by 2–3°C, the deep placement of the colony appears to confer on it considerable thermal stability. The colony is ventilated through a remarkable above-ground structure, consisting of a prominent chimney that can be as much as 2 m high, that communicates in a circuitous way through the colony to a number of small entrance holes at the surface of the ground. Ventilation of the colony appears to be driven in at least three ways. Under near still air conditions, free convection currents may translocate air from the colony into the chimney, whence it is wafted to the outside air. The net flow of air in this circumstance is unidirectional, moving into vent holes in the surface of the mound, through the colony, and finally out the chimney. During moderately windy conditions, induced flow appears to draw air out the chimney mouth, and appears to be the most important ventilatory mechanism: flow of air in this circumstance also is predominantly unidirectional. During gusty or turbulent wind conditions, outside air can be driven into the chimney mouth. Flow of air can be opposite in direction to that predicted for induced flow, and can even be tidal. On average, about 80 min are required for 95% of colony air to be exchanged with the surrounding air. The ventilation of these colonies is probably solely for gas exchange – altering flow of air at the chimney has little effect on colony temperature.

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