ECOTROPICA 12: 27–33, 2006


# RESPIRATION RATES OF SOIL INVERTEBRATES FROM TEMPERATE AND TROPICAL ZONES AS MEASURED BY INFRARED GAS ANALYSIS

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*Abstract*: A computerized photosynthesis measuring system based on infrared gas analysis was modified to measure the respiration (i.e., $CO_2$ production) of small soil invertebrates. By changing the air flow of the system to a closed-circle mode, small amounts of $CO_2$ produced by soil animals became measurable through accumulation in the circulating air. The $CO_2$ production of various soil invertebrates such as earthworms, termites, and millipedes from the temperate zone (Germany), and from a tropical forest in the Brazilian Amazon, was assessed. Respiration rates of animals from the tropics were in the range of 26.8–1141.8 µl $CO_2$ per hour and gram biomass (fresh mass) and were comparable to respiration rates of soil invertebrates from the temperate zone. Respiration rates varied between and within taxa and depended on the activity of the animal. *Accepted 10 March 2006.*

*Key words*: *$CO_2$ production*, *Diplopoda*, *IRGA*, *Isopoda*, *respiration*, *soil fauna*, *tropical rain forest*.

## INTRODUCTION

Invertebrates are an important structural component of the soil compartment and fulfill essential functions within the ecosystem (Scheu and Setälä 2002). The soil fauna is of major importance for litter decomposition and thus for the cycling of carbon and many plant nutrients in temperate ecosystems (Petersen & Luxton 1982). The same has been demonstrated for tropical forest systems (Heneghan *et al.* 1999, Höfer *et al.* 2001). Although mineralization of organic matter from soil and litter is mainly attributed to the activity of the soil microflora, it is widely accepted that this process is strongly influenced by the soil fauna, e.g., via comminution during the feeding activity of soil meso- and macro-fauna on litter. However, quantitative data on the direct contribution of soil invertebrates to carbon release via respiration are scarce.

The aim of our investigation was to measure the amount of carbon that is directly contributed by the soil fauna. Therefore a device to measure the small amounts of $CO_2$ released by soil invertebrates was developed. A commercially available portable photosynthesis measuring system, based on an infrared gas analyzer (IRGA) and designed to quantify the $CO_2$ uptake of single plant leaves, was modified in such a way that the $CO_2$ production of soil invertebrates could be measured.

The work was performed at the laboratories of ECT Oekotoxikologie in Flörsheim, Germany, and at the research station of the Empresa Brasileira de Pesquisa Agropecuária, Embrapa Amazônia Ocidental, located in the Brazilian state of Amazonas. It was part of the project "soil fauna and litter decomposition in primary and secondary forest and a mixed culture system in Amazonia" carried out within the German-Brazilian scientific co-operation program "Studies on human impact on floodplains and forests in the tropics, SHIFT" (Höfer *et al.* 2001).

## MATERIAL AND METHODS

*$CO_2$ Analysis.* We used a portable photosynthesis measuring system HCM-1000 (Heinz Walz GmbH, Effeltrich, Germany) consisting of an infrared gas analyzer (IRGA), a flow-controlled peristaltic air pump, a mass flow meter, and a measuring chamber (cuvette). The system is controlled via a computer. It works in an open-flow mode at a flow rate of 1000 ml $min^{-1}$ and can either operate in a differential or in an abso-

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lute mode. The former measures the difference between the $CO_2$ concentration of two separate streams of ambient air, one of which passes through the cuvette that contains a leaf (measuring stream) while the other (reference stream) is led directly to the IRGA. In the latter mode, the air of the reference stream passes through a column filled with soda lime to scrub off the $CO_2$ before being measured. This mode is usually chosen to determine the $CO_2$ concentration of the ambient air.

To measure the small amounts of $CO_2$ that are produced by soil invertebrates such as millipedes, the air flow of the measuring stream was changed to closed-circuit mode. The use of the open-flow mode, with required flow rates of 1000 ml $min^{-1}$, was not appropriate here since the small amounts of $CO_2$ produced by soil organisms would not increase the $CO_2$ concentration sufficiently to be detected. By using a closed-circuit mode, the $CO_2$ produced by soil organisms could accumulate in the air. The reference stream was also installed in closed-circuit mode, passing through soda lime. Thus there were two separate closed circuits, a measuring and a reference circuit, each driven by a small peristaltic pump at a flow rate of 1000 ml $min^{-1}$ (Figure 1). The tubing (inner/outer diameter 4/6 mm) of the pneumatic connections between the IRGA and the cuvette was made of a fluoroelastomer (viton®, DuPont) to avoid $CO_2$ uptake by, or release from, the tubing during changes of $CO_2$ concentrations in the airstream.

*Cuvette*. The cuvette (measuring chamber) was originally designed to measure the $CO_2$ uptake of a single leaf. It is equipped with temperature and humidity sensors, an oscillating fan to ensure even air circulation within the cuvette, and a Peltier element to adjust to a stable temperature within the cuvette.

To provide appropriate conditions for the measurement of the $CO_2$ production of small soil invertebrates such as earthworms or termites the cuvette was modified. The original clamp to hold the leaf was replaced by a cylindrical test chamber made out of polyacetate (POM) that could be closed air-tight by a screw-top equipped with an o-ring seal.

*Calibration of the system*. The IRGA measured the concentration of $CO_2$ in an airstream as volumetric ppm. From this value the total amount of $CO_2$ could only be calculated if the entire volume of the closed system (Vt) was known. To calibrate the system, a calibration volume ($V_c$) of 100 µl $CO_2$ was injected through the tubing into the system via a micro-syringe. This procedure was repeated several times. The $CO_2$ concentration in the closed circuit increased by 322.6 ppm per 100 µl $CO_2$ added. From this increase the total

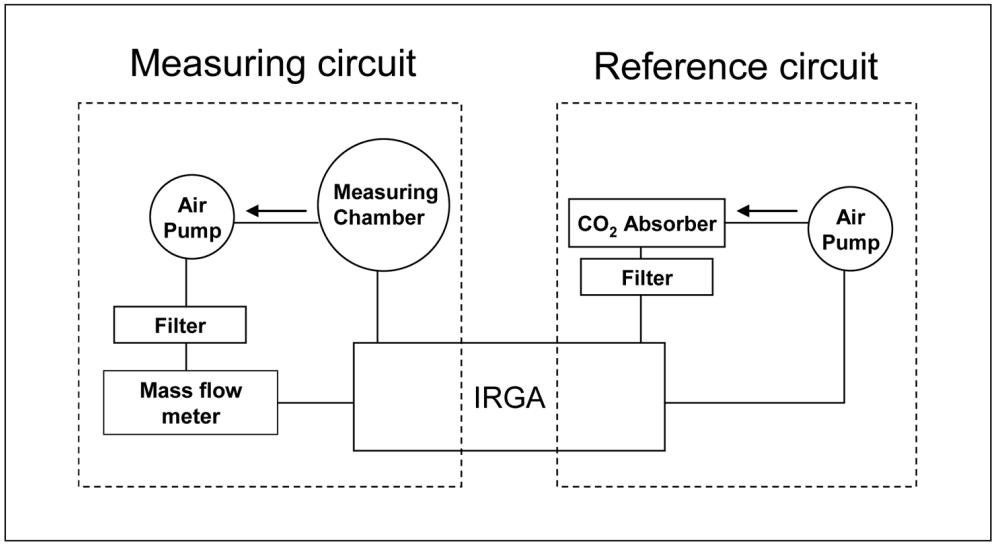


FIG. 1. Scheme of the pneumatic connections in the device to measure the respiration of small soil invertebrates.

volume of the circuit was calculated according to equation (1).

$$(1)\quad V_t = \frac{10^6 \mu l \, x V_c}{322.6 \mu L \, CO_2 \, x 1000}$$

*Sampling of soil fauna*. Soil invertebrates from the temperate zone were collected in the field near Flörsheim, Germany and were measured on the same day. Enchytraeids (*Enchytraeus albidus*) were taken from own breeding cultures. Soil animals from the tropical zone were collected in the field by hand-sorting leaf litter from the ground of a rainforest near Manaus, Amazonia, Brazil. These were diplopods, isopods, beetles, and others. Termites were sampled by breaking up part of a termite nest. All soil animals from the tropics were held in the laboratory at 26–28°C in boxes filled either with soil and litter or with nest material (termites) for up to 4 days prior to measuring (except for termites which were measured on the day of collection).

*Respiration measurements*. Shortly before the start of the measurements, either single animals or groups of 5 to 45 specimens of the same species were weighed and placed in a perforated container (35 mm film PE-box). The container was then put into the test chamber which was continuously flushed with air in a closed circuit. Film boxes with animals to be measured could be prepared separately beforehand, providing a quick and easy exchange of boxes from the test chamber.

The respiration of the animals led to an increase in the $CO_2$ concentration in the air of the closed circuit. During the measurements, the relative humidity of the air in the closed system was in the range of 55–75% for the termites and 80–95% for the other taxa. The temperature inside the test chamber was adjusted to 31°C for termites and to 28°C for the other tropical taxa. For fauna from the temperate zone the temperature was kept at 20°C. Gradients of temperature or $CO_2$ concentration inside the test chamber were avoided because of the flow rate and additional ventilation by the internal vibrating fan. Enchytraeids were placed on a small agar disk to avoid desiccation during measurement.

Each single animal or group of animals was measured one to four times, each measurement-period lasting for 10 minutes. Within each period the $CO_2$ concentration, air temperature, relative humidity of the air, and the flow rate were measured and recorded every 30 seconds. The increase in $CO_2$ concentration within each 10-minute period was divided by ten to achieve the average increase rate per minute ($\Delta CO_2$). Between two consecutive measurements, and before putting in a new box with animals, the test chamber was opened up and flushed with ambient air for a few seconds to achieve comparable $CO_2$ concentrations at the starting point of each measurement. Measurements with an empty test chamber (and empty film box) were performed before and after each measurement of animals to assess possible leaks or base-line drift of the analyzer.

Due to the size of the large tropical earthworm of the family Glossoscolicidae we used a test chamber with a volume of 0.5 l and changed the mode of respiration measurements from closed-circuit to open-flow conditions.

*Calculation of faunal respiration rate*. Respiration rate in closed-circuit mode was calculated using equation (2):

$$(2)\quad V_{CO_2} = \frac{\Delta CO_2 \, x V_t \, x \, 60}{m}$$

$V_{CO_2}$ = Respiration rate [µl $CO_2$ $h^{-1}$ $g^{-1}$ fresh mass]
$\Delta CO_2$ = Increase in $CO_2$ concentration [ppm/min]
$V_t$ = Total volume of closed system [L]
$m$ = Biomass of the animal [g fresh mass]

Respiration rate in open-flow mode was calculated using equation (3):

$$(3)\quad V_{CO_2} = \frac{\Delta CO_2 \, x V_{air} \, x \, 1000}{m}$$

$V_{CO_2}$ = Respiration rate [µl $CO_2$ $h^{-1}$ $g^{-1}$ fresh mass]
$\Delta CO_2$ = Difference in $CO_2$ concentration in the air before and after passage through the test chamber [ppm]
$V_{air}$ = Flow rate of air through the test chamber [ml/min]
$m$ = Biomass of the animal [g fresh mass]

## RESULTS AND DISCUSSION

All animals survived the measurements without any visible damage. Respiration rates, calculated from the increase in $CO_2$ concentration over a time period of ten minutes with measurements every 30 seconds, were almost linear. The base-line drift of the system was minimal (< 0.03 ppm $min^{-1}$) while measuring animals from the temperate zone but it increased during measurements of the tropical fauna (up to 2.1 ppm $min^{-1}$). Therefore respiration rates of the tropical fauna were corrected for the drift. Results are given in Tables 1 and 2. For all animals except the tropical diplopod of the family Platyrhacidae, that was permanently moving around throughout the measurements, the values represent average respiration activity of animals while active and at rest.

The lowest observed $CO_2$ production of the tropical forest taxa was 26.8 µl $CO_2$ $h^{-1}$ $g^{-1}$ for a beetle of the family Passalidae at rest. Respiration increased by a factor of seven to 191.2 µl $CO_2$ $h^{-1}$ $g^{-1}$ when the beetle was active. Bartholomew & Casey (1977) reported values for a beetle from the family Passalidae ranging from 213 µl $h^{-1}$ $g^{-1}$ at rest to 551–3495 µ $h^{-1}$ $g^{-1}$ when active (calculated from $O_2$ uptake assuming a respiratory quotient of RQ = 1). The body mass of these beetles was about half that of the species we measured. Since the respiration rate was calculated on the basis of the individual biomass fresh weight, the amount of metabolic inactive biomass (e.g., the chitin carcass) may vary considerably between taxa and thus affect the calculated respiration rate. Moreover, discontinuous gas exchange patterns, such as have been described for various insects (e.g., by Gibbs & Johnson 2004, Marais *et al*. 2005), may also apply to the species we investigated. This may explain the different values we observed when measuring the respiration of a true bug from the temperate zone during several subsequent periods of 3 to 6 minutes each over a time period of 90 minutes (Figure 2). On the other hand, the $CO_2$ concentration usually increased linearly over time during the 10-minutes measurement periods with $CO_2$ measurement every 30 seconds. The measurement periods of 10 minutes, however, may have been too short to detect such different respiration patterns.

Termite soldiers of the genus *Nasutitermes* and grasshoppers (Orthoptera) always produced higher amounts of $CO_2$ compared with other taxa (Table 1), with an average of 643.6 µl $CO_2$ $h^{-1}$ $g^{-1}$ (termites) and 672.3 µl $CO_2$ $h^{-1}$ $g^{-1}$ (grasshoppers).

TABLE 1. Respiration rates of different taxa of tropical soil invertebrates from Amazonia.

| | No. per group | Total number | Mean biomass [g] | Respiration [µl $CO_2$ $h^{-1}$ $g^{-1}$] mean ± S.D. |
|---|---|---|---|---|
| Annelida: Oligochaeta | | | | |
| 1 *Pontoscolex corethrurus* | 1 | 2 | 1.344 / 1.061 | 172.4 / 170.3 |
| 2 *Rhinodrilus priollii* | 1 | 2 | 71.4 / 76.7 | 48.5 / 43.8 |
| Arachnida: Opiliones | | | | |
| 3 Gen. sp. | 5 | 5 | 0.0492 | 363.3 |
| Crustacea: Isopoda | | | | |
| 4 Gen. sp. | 5–10 | 60 | 0.0531 | 291.3 ± 288.49 |
| Myriapoda: Diplopoda | | | | |
| 5 *Trigoniulus coralinus* | 1 | 9 | 0.636 | 234.1 ± 66.4 |
| 6 *Asiomorpha coarctata* | 5 | 5 | 0.251 | 352.7 |
| 7 *Chelodesmidae* Gen. sp. | 1 | 4 | 0.234 | 279.9 ± 63.7 |
| Insecta: Blattodea | | | | |
| 8 Gen. sp. | 1 | 2 | 0.215 / 0.204 | 404.5 / 534.0 |
| Isoptera | | | | |
| 9 *Nasutitermes* sp. (soldiers) | 45 | 225 | 0.0025 | 643.56 ± 118.8 |
| 10 *Nasutitermes* sp. (workers) | 45 | 225 | 0.0052 | 489.6 ± 82.0 |
| 11 *Labiotermes* sp. (soldiers) | 4–45 | 79 | 0.0167 | 289.5 ± 33.7 |
| Caelifera | | | | |
| 12 Gen. sp. | 1 | 5 | 0.363 | 672.3 ± 231.9 |
| Heteroptera: Geocorisae | | | | |
| 13 Gen. sp. | | | 0.185 | 1141.8 |
| Coleoptera: Passalidae | | | | |
| 14 Gen. sp. (at rest) | 1 | 1 | 1.62 | 26.8 |
| 15 Gen. sp. (active) | 1 | 1 | 1.62 | 191.2 |

TABLE 2. Respiration rates of different taxa of soil fauna from the temperate zone (Germany).

| | No. per group | Total number | Mean biomass [g] | Respiration [µl $CO_2$ $h^{-1}$ $g^{-1}$] mean ± S.D. |
|---|---|---|---|---|
| Annelida: Enchytraeidae | | | | |
| 1 *Enchytraeus albidus* | 10 | 10 | 0.0062 | 723.0 |
| Crustacea: Isopoda | | | | |
| 2 *Porcelio scaber* | 1 | 2 | 0.109 | 197.1 |
| Insecta | | | | |
| Heteroptera: Geocorisae | | | | |
| 3 Gen. sp. | 1 | 1 | 0.186 | 1476.0 |
| Coleoptera: Carabidae | | | | |
| 4 Gen. sp. | 1 | 1 | 0.213 | 285.6 |
| Coleoptera: Scarabaeidae | | | | |
| 5 *Geotrupes* sp. | 1 | 1 | 0.131 | 156.0 |
| Lepidoptera | | | | |
| 6 Gen. sp. (larva) | 1 | 1 | 0.233 | 1017.6 |
| Lepidoptera: Geometridae | | | | |
| 7 Gen. sp. (larva) | 1 | 1 | 0.051 | 904.8 |
| 8 Gen. sp. (larva) | 1 | 1 | 0.095 | 1117.8 |
| 9 Gen. sp. (larva) | 1 | 1 | 0.075 | 1158.0 |

Lower average $CO_2$ production was found for termites, 310.9 µl $h^{-1}$ $g^{-1}$ (soldiers of *Labiotermes* sp.), 489.6 µl $h^{-1}$ $g^{-1}$ (workers of *Nasutitemes* sp.), 268.1 µl $h^{-1}$ $g^{-1}$ (workers of *Labiotermes* sp.), and for isopods and diplopods with 291.3 µl $h^{-1}$ $g^{-1}$ and 240.1 µl $h^{-1}$ $g^{-1}$, respectively.

Nunes *et al.* (1997) found that the RQ of termites was different depending on the quality of food, and Hanne (2001) was able to show that the $CO_2$ production of different termite species was related to the quality of their food.

The very high $CO_2$ production observed with true bugs from the temperate zone (1476.0 µl $h^{-1}$ $g^{-1}$) and the tropics (1141.8 µl $h^{-1}$ $g^{-1}$) may be explained by the fact that many true bugs feed on phloem liquid, which is rich in sugars and can be easily respired.

Respiration rates of the tropical diplopods were in the range found for diplopods from the temperate zone (Schallnaß 1989), while respiration of tropical isopods was always slightly higher compared with isopods from the temperate zone.

The average respiration of other taxa from the temperate zone was 156.0 µl $h^{-1}$ $g^{-1}$ for a dung beetle (*Geotrupes stercorosus*), 285.6 µl $h^{-1}$ $g^{-1}$ for a carabid beetle (Carabidae), and 1476.0 µl $h^{-1}$ $g^{-1}$ for a true bug (Table 2).

The respiration rate found for earthworms seemed to decrease with increasing biomass (i.e., with decreasing ratio between body surface area and biomass). The same tendency was also observed by Mendes & Valente (1953), who studied the respiration rate of three earthworm species. The respiration rate of *Pontoscolex* sp. (small size) ranged from 130 to 284 µl $h^{-1}$ $g^{-1}$, dropping to 60–271 µl $h^{-1}$ $g^{-1}$ for *Pheretima hawayana* (medium size), and 38–109 µl $CO_2$ $h^{-1}$ $g^{-1}$ biomass for *Glossoscolex* sp. (large size). Further work from tropical regions (e.g., Mishra & Dash 1984) is not comparable with the data presented here due to different methods and/or measurement units (e.g., no mass data available).

Bolton (1970) measured the respiration of the earthworm species *Dendrobaena rubida* and *Lumbricus castaneus* at 10 °C and reported values of between 75 and 100 µl $CO_2$ $h^{-1}$ $g^{-1}$. Larger lumbricid species like *Lumbricus terrestris* showed values of between 70 and 90 µl $CO_2$ $h^{-1}$ $g^{-1}$; due to a diurnal rhythm respiration can be higher during certain times of the day (Edwards & Bolton 1996). Uvarov (1998) showed the

expected temperature dependence of the respiration of *Dendrobaena octaedra*, with respiration rates of 32.3 µl $CO_2$ $h^{-1}$ $g^{-1}$ at 5°C and 148.5 µl $CO_2$ $h^{-1}$ $g^{-1}$ at 25°C.

Based on the examples of soil fauna measured here we found no correlation between biomass and respiration. The lack of a correlation may, however, be due to the low number of animals assessed, and also to the variability in $CO_2$ production depending on different phases of activity and rest of the animals.

In general, data on soil invertebrate respiration in the literature are scarce, especially for tropical regions. Moreover the data are difficult to compare, due to the use of different methods and, even more importantly, different measurement conditions. For example, it often is not known whether the conditions during measurements, such as temperature, moisture, and light, induce stress in the organisms, or whether the animals were active or at rest during the measurements. These different measurement conditions may contribute considerably to the observed high variability of $CO_2$ production within species of the same taxa usually described in the literature (e.g., Marais *et al*. 2005). Also, the duration and frequency of measurements can affect the results, especially if the animals show discontinuous or cyclical respiration patterns. In a study on the gas exchange patterns of insects, Marais *et al*. (2005) compared literature data of 99 species with their own results of a further 19 sample species, and found that of 99 species, 35 showed cyclical gas exchange. Moreover, the respiration rate of active animals can change over time, as was shown for spiders in a treadmill by Schmitz (2005). These spiders often showed a burst-like maximum $CO_2$ production at the start of activity, which then decreased to a steady state value or decreased constantly. Since our measurements represent means of respiration rates recorded over 10-minute periods, such differences in respiration patterns could only have been detected if respiration rates happened to change considerably within this short period of time. To estimate the contribution of soil fauna respiration to the overall carbon loss from tropical soil, however, such a fine differentiation of respiration patterns may not be necessary.

Our results of soil fauna $CO_2$ production indicate that the direct contribution of the soil fauna seems to be negligible when considering the overall amount of $CO_2$ released from the soil of the tropical primary forest area where the study species were collected. Based on the average respiration of the mineral soil at 0–5 cm depth (1.64 µl $CO_2$ $h^{-1}$ $g^{-1}$ soil dry weight) measured under laboratory conditions,

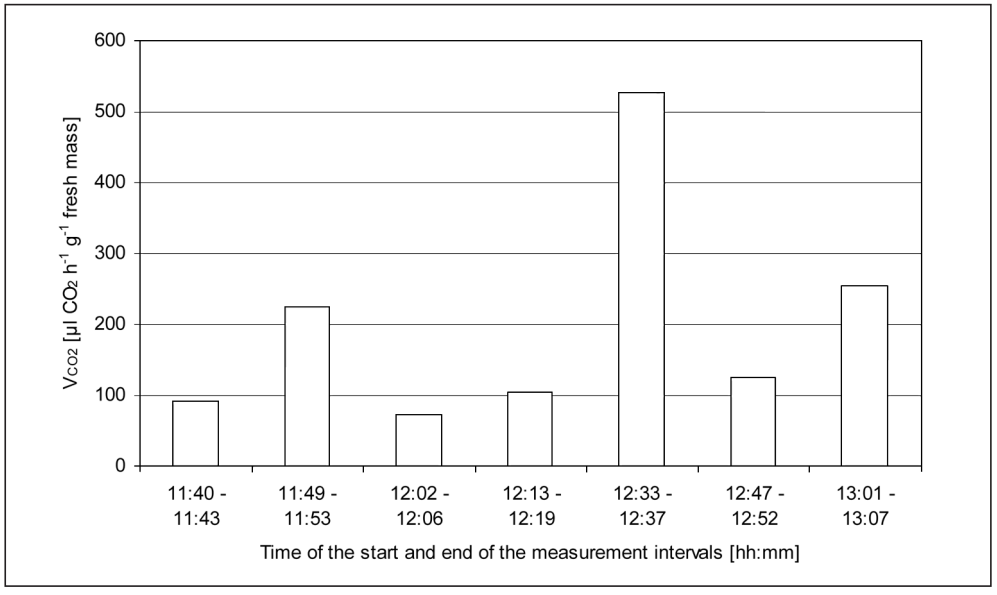


FIG. 2. Mean $CO_2$ production of a true bug from the temperate zone during several subsequent measurement intervals.

the yearly loss of carbon via soil microbial respiration is estimated to total about 0.718 kg $m^{-2}$ (B. Förster, unpublished data). Based on the soil fauna biomass of 2.7 g dry mass $m^{-2}$ (Höfer *et al.* 2001), the yearly loss of carbon from the soil system through respiration of the soil macrofauna would total only 0.013 kg $m^{-2}$.

## CONCLUSION

Generally, respiration rates of the soil fauna from tropical and temperate regions were in the same range, except that tropical isopods produced slightly more $CO_2$ than those from the temperate zone. $CO_2$ production differed between taxa and also within taxa. There was some indication that discontinuous patterns, irrespective of whether the animal is active or at rest, contributed to the variability of respiration rates. To reduce such sources of variability it is recommended to standardize the environmental conditions during the measurements as far as possible and to choose measurement periods long enough to detect differences in the respiration pattern. The IRGA equipment chosen has the potential to fulfill these requirements and proved to be appropriate to measure the $CO_2$ production of small soil invertebrates through $CO_2$ accumulating in a closed circuit. Irrespective of the observed variability in the results, it can be concluded that the direct contribution of the soil fauna to the overall $CO_2$ release from soil into the air is negligible compared to the $CO_2$ released via microbial respiration.

## ACKNOWLEDGMENTS

These studies were conducted as part of the SHIFT program based on the German-Brazilian governmental agreement (project ENV 52). Authors are grateful to the German Bundesministerium für Bildung und Forschung (BMBF) and the Brazilian Conselho Nacional de Desenvolvimento Científico e Technológico (CNPq) for funding the studies (under the BMBF grant number 0339675). Special thanks go to Dr. Stefan K. Hetz and to an anonymous referee for their helpful comments on the manuscript.

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