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Changes in soil quality after subsequent establishment of *Chromolaena odorata* fallows in humid savannahs, Ivory Coast

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ABSTRACT

In the buffer zone of the Lamto Reserve, a protected area located in the forest-savannah transitional zone in central Ivory Coast, the exotic shrub *Chromolaena odorata* has invaded abandoned fields and degraded forests. As a result, they have turned into thickets that are used by local farmers as natural fallows to enhance soil fertility for food production. However, information about their impact on soil is scanty and investigations focusing exclusively on baseline data on *C. odorata* fallows in humid savannahs are still lacking. This study was designed to assess changes in soil physical, chemical and biological properties after the establishment of *C. odorata* fallows in humid savannahs of Ivory Coast. Sampling sites were selected such that a portion of *C. odorata* fallow was located next to the shrub savannah, the most common natural ecosystem in the area. Results revealed a rise of soil organic carbon (+27.9%), total nitrogen (+36.7%), total phosphorus (+56.8%), extractable calcium (+68.3) and magnesium (+140.3%) in the first 10 cm of soil beneath the *C. odorata* fallow relative to the savannah. Furthermore, the fallow was associated with high N-mineral pool as N-NO_3^- and N-NH_4^+ content increased at +72.5% and +71.5%, respectively. The infiltration capacity of water under *C. odorata*-based fallow was markedly high and soil macroinvertebrates, mainly earthworms, showed significant increases in density and biomass. The large quantity of good quality standing biomass produced by *C. odorata* is likely the main factor controlling the improvement of soil quality. The results suggest that there are merits for the integration of *C. odorata* fallow in a cropping system for sustainable food production in the buffer zone of Lamto Reserve. This can also help to reduce pressure on forest islands.

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1. Introduction

Chromolaena odorata is an invasive deep-rooted shrub recorded as part of the 100 worst invasive species in the world (IUCN, 2001) and spreads throughout humid and sub humid agricultural landscapes in Sub-Saharan Africa. Initially introduced in Ivory Coast around 1931 as a cover crop in rubber and palm-oil tree plantations (Gautier, 1992), this shrub colonized very rapidly over the humid and sub humid parts of the country characterized by a minimum annual rainfall of 1100 mm and a dry season no longer than 5 months. Due to its rapid growth, this shrub has created dense stands along forest margins and has profoundly altered landscapes of Ivory Coast. For instance, in the southern areas of the country, most secondary forests have degenerated to *C. odorata* thickets (Slaats, 1992). Because of the high rate of disturbance

in terrestrial ecosystems in Ivory Coast, *C. odorata*-based fallows are currently the most common agro-ecological units in the humid and sub-humid areas, which are being sought after by farmers as arable land.

In Ivory Coast, the forest-savannah transition and humid savannah zones are expanding due to increasing proportion of derived savannah, where *C. odorata* represents the dominant fallow species, like in Ghana (Amanor, 1996). Soils in savannah ecosystems are mostly infertile, as they are characterized by low organic matter, phosphorus, and nutrient content along with the presence of low activity clay (Juo et al., 1995). Consequently, there have been quite a number of studies over the past decade aimed at improving the productivity of fallows with the help of legumes (Anthofer and Kroschel, 2005; Barrios et al., 2005; Bünemann et al., 2004; Tian et al., 2000a; Ysuf et al., 2009). Legume-based technologies for fertility management in small-scale farming systems were relatively unsuccessful in the past, as legume species were mostly exotic and costs related to their management were unaffordable to farmers. Alternatively, *C. odorata* fallows that are already present in the systems and reported by farmers to indicate soil fertility status (Adjéi-Nsiah et al., 2004; Kouassi, 2010; Yonghachea, 2005) are worth studying in the context of sustainable

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agriculture intensification. An excellent introduction to the subject was highlighted by Roder et al. (1995) who qualified *C. odorata* as a good fallow species considering its fast expansion after crop harvest, high biomass production, weed suppression and fast decomposition rate.

However, *C. odorata* is mostly regarded as a weed (IUCN, 2001), and any attempt to consider the management of derived fallows for sustainable agriculture intensification in small scale farming systems, should be preceded by an assessment of their impact on soil quality. Although fallows invaded by *C. odorata* are subject to speculations on their role in soil fertility improvement for several decades, very few studies have documented the contribution of the exotic shrub to soil fertility improvement in humid savannahs. Partial information on the positive impact of *C. odorata*, in natural fallows, on soil chemical properties has been stressed by studies in West (Slaats, 1992) and Central Africa (Koutika et al., 2002, 2004) forest margins. In the forest-savannah transitional landscapes where they are predominant, recent investigations have highlighted the association of *C. odorata* fallows with higher topsoil N status, earthworms, enzyme activities and plant nutrient availability (Koné et al., 2012a,b; Norgrove et al., 2008). However, the holistic approach of soil quality assessment that implies the consideration of soil chemical, physical and biological properties beneath *C. odorata* fallows as compared to the baseline system is most likely to provide much better insights into their role in soil fertility improvement. Therefore, this study aimed to find out whether or not soil quality was improved by *C. odorata* fallow by assessing changes in soil physical, chemical and biological properties after the establishment of those fallows in humid savannahs of Ivory Coast. Ultimately, the study intended to contribute to the sustainable management of soils in the buffer zone of the Lamto reserve in order to reduce the pressure of farmers on forest patches for agricultural purposes.

2. Materials and methods

2.1. Study site

The present study took place in May 2003 in the buffer zone of the Lamto Reserve (6°13' N and 5°20' W), a protected area located in the forest-savannah transitional zone in central Ivory Coast (Fig. 1). The area has a bimodal rainfall distribution and received on average 1200 mm of rain and mean temperature about 27 °C in 2003. The dry seasons last from November to March and from July to August.

Sampling sites were selected in such a way that a portion of *C. odorata* fallow was located next to the shrub savannah, the most common natural ecosystem in the area. The first site was established in a 17-year-old fallow colonized by the invading weed *C. odorata*, subsequent to yam cropping in the shrub savannah. The second site was located 30 m away from the first and referred to as a shrub savannah composed of 34 species bulked into 20 families of angiosperma (15 dicotyledons and 5 monocotyledons) according to Koné (2009). The herbaceous stratum was characterized by the presence of *Hyparrhenia diplandra* and *Imperata cylindrica*, while *Cussonia barteri*, *Crossopteryx febrifuga*, *Terminalia glaucescens*, *Nauclea latifolia*, and *Annona senegalensis* were the main shrubs. The most important families were Papilionaceae and Asteraceae. In spite of its apparent relative homogeneity, the *C. odorata*-dominated fallow comprised more species that amounted to 78 and comprised 40 families of angiosperma (32 dicotyledons and 8 monocotyledons). According to Koné (2009), the most representative group in the fallow was the leguminous bulked into 3 families: Papilionaceae, Cesalpiniaceae, Mimosaceae. Moreover, the fallow site was characterized by the presence of species of secondary forest (*Albizia adianthifolia*, *Albizia zygia*, *Antaris toxicaria*, *Holorrhena floribunda*, and *Milicia excelsa*) and degraded areas (*Trema guineensis*, *Malancantha alnifolia*, *Ficus sur*, *Ficus vallis-choudae*, and *Elaeis guineensis*). Soils at both sites are Alfisols with a sandy loam upper layer (0–30 cm) overlying sandy clay (30–70 cm) and stony (>70 cm) horizons (Koné et al., 2008).

2.2. Experimental layout

Sampling sites of similar size (84 m × 60 m) were selected in two contrasting ecosystems common to the study area: shrub savannah and *C. odorata* fallows. In order to make allowance for spatial variability due to soil heterogeneity, a randomized complete block design, common in agricultural and other studies (Bathke et al., 2010), was used. It consisted of 3 blocks comprising 6 plots measuring 24 m × 8 m each and selected in each site (Fig. 2). A 4 m-wide alley separated each block while a distance of 2 m was between the plots. The experimental design was similar at both sites, where each plot was further split into 3 subplots (8 m × 8 m) to host specific measurements (Fig. 2).

2.3. Aboveground and root biomass

Plant biomass determination was carried out considering *C. odorata* and *H. diplandra* as the most representative flora species covering more than 60% of the soil in the fallow and the savannah, respectively (Koné, 2009). Prior to soil collection and earthworm sampling, the standing biomass of *C. odorata* and *H. diplandra* was sampled with a 1 m² quadrat, in 3 subplots: 1 chosen randomly per block yielding a total of 9 replicates per site. Plant roots were carefully collected using a 25 × 25 × 40 cm soil monolith within the 1-m² quadrat. Plant materials such as green material (leaves), dead residues (mulch), and roots ($\theta < 2$ mm and $\theta > 2$ mm) collected were oven-dried at 60 °C for 72 h and weighed. A 20 g subsample of leaves and fines roots ($\theta < 2$ cm) was finely ground and stored in plastic bags for further chemical analyses.

2.4. Soil physical properties

Soil water infiltration capacity in both sites was determined using the single ring infiltrometer technique (Anderson and Ingram, 1993) in subplot 2. A vertical metal single ring (diameter 25 cm, length 40 cm) was carefully driven into the soil to a depth of about 15 cm. It was thereafter filled up with water, the level of which was measured at 5, 10, 15, 20, 30, 40, 50, 60 and 75 min. The cylinder was refilled when the level had dropped to about 10 cm.

Bulk density of the top layer was estimated using a 6 cm diameter and 10 cm height metal cylinder in subplot 2. The fine fraction (clay and silt) was determined using the Robinson Pipette method (Anderson and Ingram, 1993).

2.5. Soil samples and macroinvertebrates

The abundance and biomass of soil macroinvertebrates were systematically measured in subplots 3 using a modified TSBF method (Anderson and Ingram, 1993). It consisted of extracting one soil monolith (25 × 25 × 20 cm) with an iron frame toward the middle of each plot. Soil organisms were collected by hand-sorting in trays and preserved in 4% formaldehyde solution (earthworms) and 70% alcohol (other organisms).

Similarly, soil samples were collected with augers at 9 different points distributed within the subplot, in the first 10 cm layer and thoroughly mixed into composite samples. They were then air-dried, crushed, sieved at 2 mm and stored in plastic bags for further analyses.

2.6. Analytical methods

2.6.1. Plant materials

Organic carbon was determined after mineralization using a sulfochromic solution (Walkley and Black, 1934), while total nitrogen was obtained using the standard Kjeldahl digestion method. Phosphorus content was measured by colorimetry after a nitriperchloric digestion and subsequent molybdenum-blue colour development (Olsen and Sommers, 1982). Major cations were extracted using ammonium

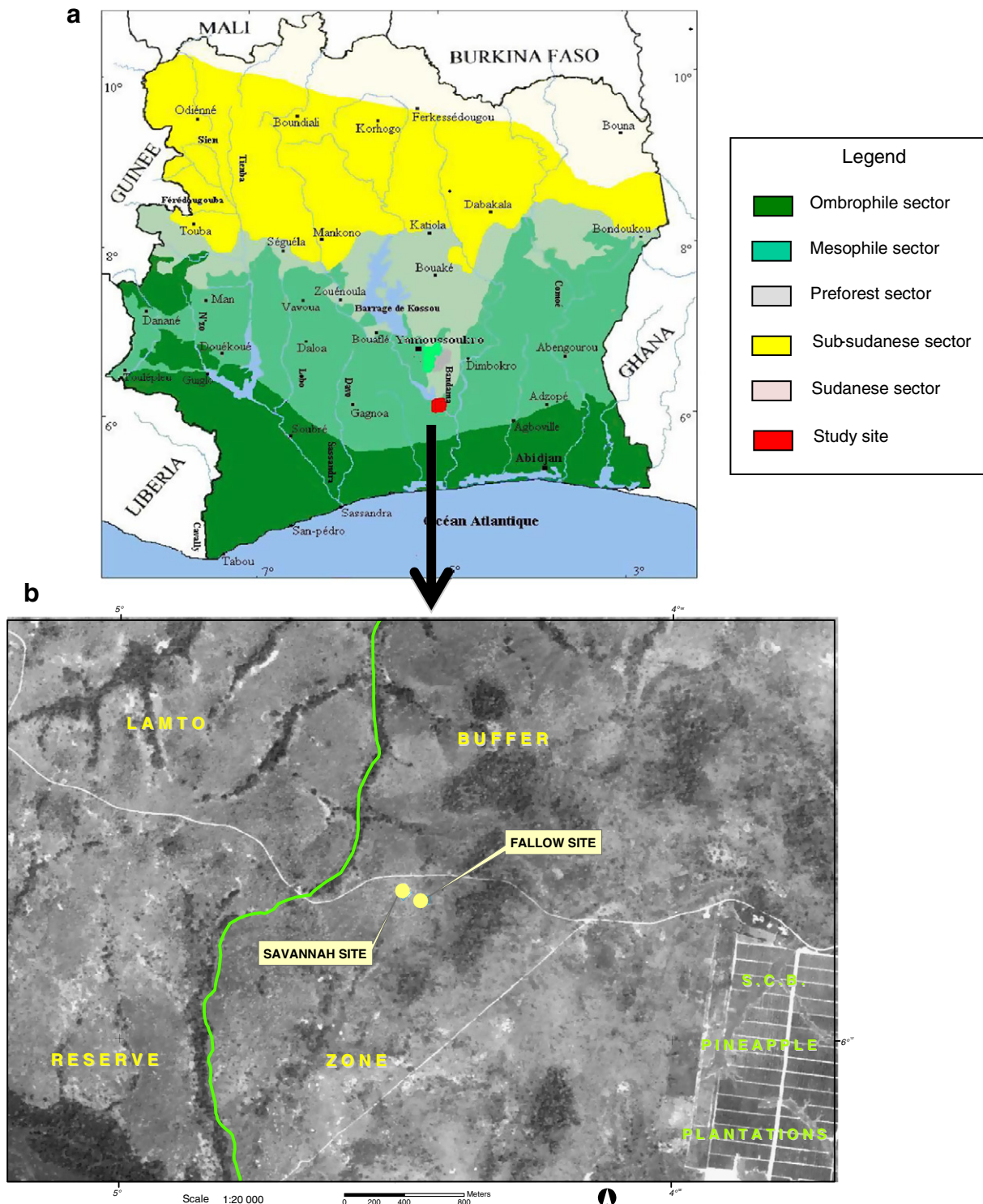


Fig. 1. (a) Map of Ivory Coast showing (b) the situation of savannah and fallow sites within the study area.

acetate buffer (pH 7) and determined using atomic absorption spectrophotometry techniques.

2.6.2. Soil samples

Soil pH was determined in soil:water (1:2.5) suspension. Available phosphorus (available P) was extracted according to the Olsen–Dabin method (in a mixture of NaHCO_3 and NH_4F , at pH 8.5) and total phosphorus (total P) was extracted in a mixture of HNO_3 and HClO_4 (Olsen and Sommers, 1982). Exchangeable bases were extracted using the

standard ammonium acetate (pH 7) buffer and determined by atomic absorption spectrometry. Cation exchange capacity (CEC) and texture (clay + silt proportion) were determined using methods recommended by Anderson and Ingram (1993). For the texture measurement, organic matter was destroyed using hydrogen peroxide and soil was suspended in Na-hexametaphosphate solution.

Soil organic carbon (SOC) and total nitrogen (total N) were determined using near-infrared reflectance spectroscopy (NIRS) techniques. The method was based on a close relationship between the

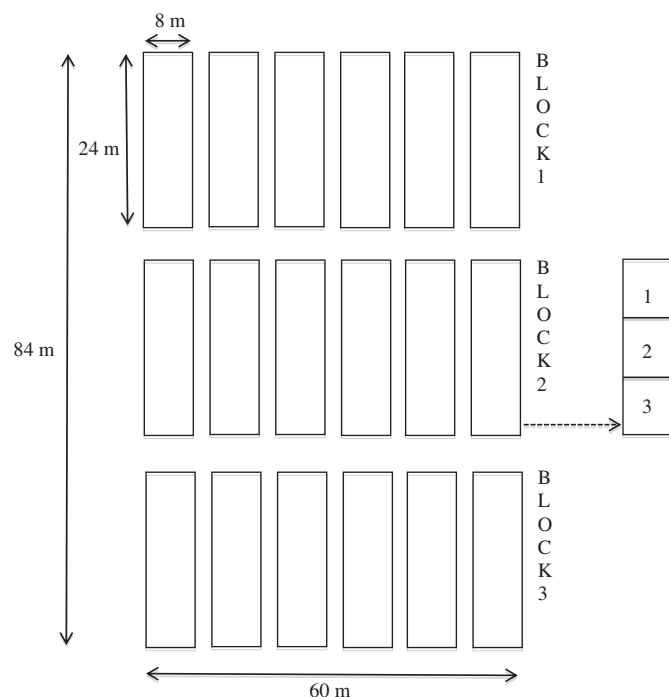


Fig. 2. Experimental layout of a study site.

spectral absorbance and sample biochemical composition (Dalal and Henry, 1986; Ludwig et al., 2002; McCarthy et al., 2002; Morra et al., 1991). The samples were analysed using a spectrophotometer, FOSS 5000 model (Foss NIR Systems, Silver Spring, MD, USA) at 1100–2500 nm to produce spectra with 700 data points. The spectral data obtained was recorded as the logarithm of the inverse of reflectance: $[\log (1/R)]$. It was then analysed using WinISI III-version 1.50e software (Foss NIRSystems, Infrasoft International). A reference set was selected using the most representative samples identified with the internal algorithm Winisi software, as detailed by Shenk and Westerhaus (1991). Then, the samples were analysed in an elemental micro-analyzer CHN Carlo Erba (CE Instruments, Milan, Italy) to determine soil organic C and total N. Finally, the calibration model from a reference set was applied to the spectral data of all soil samples to predict C and N contents.

Soil carbon mineralization (Cmin), which may control the amounts of available nutrients (Knoepp et al., 2000) or the organic matter degradability, was measured directly through CO₂ emission by soil micro-organisms. Seventy grams of dry soil was brought to 80% of field capacity with distilled water and put into a jar with open pipes to allow aeration. The jars were incubated in an oven at a constant temperature of 30 °C before CO₂ measurements after 7, 14, and 21 days. The easily degradable carbon was determined using an infrared CO₂ meter (Dräger Polytron IR CO₂) according to the dynamic closed chamber method (Bekku et al., 1997).

Microbial biomass C (MBC) was determined using the chloroform fumigation-extraction method (Vance et al., 1987; Horwarth and Paul, 1994). Nitrogen mineralization (Nmin) was determined by measuring the production of mineral N (N-NH₄⁺ and N-NO₃⁻) during incubation for 21 days. N-mineral contents were measured by the Nessler and phenoldisulfonic methods respectively. As for NH₄⁺, a 10 g soil sample (dry weight equivalent) was shaken with 50 ml of NaCl (1.7 M) for 30 min. Then the filtration was performed with Whatman GF/D after centrifugation for 10 min at 5100 ×g. N-NH₄⁺ was measured with a spectro-colorimeter DR/700 after adding two drops of stabiliser-disperser and 0.4 ml of Nessler reagent per 10 ml of filtrate (method HachTM, Anonymous, 1994). Concerning N-NO₃⁻, 10 g of soil sample (dry weight equivalent) was shaken with 50 ml

of CuSO₄ (0.01 M) for 30 min. This step was followed by filtration with Whatman GF/D after addition of 0.2 g of Ca (OH)₂ and MgCO₃ powder to the suspension. A quantity of 2 ml of filtrate was evaporated at 80 °C to dryness and then 2 ml of phenoldisulfonic acid, 20 ml of ultra-pure distilled water and 10 ml of concentrated NH₄OH were added (Bremner, 1965). The colour produced by phenoldisulfonic acid was also measured with a spectro-colorimeter DR/700.

2.7. Statistical analysis

The comparison of plant biomass and nutrient contents between savannah and fallow was undertaken using a *t*-test, as variables ($n=9$) from both sites were considered to be independent. To comply with the sampling design, which is a nested replication, linear mixed models were used on log-transformed data, as a Shapiro test did not show normal distribution to assess changes in soil quality. Sites were referred to as fixed effect, while blocks were designed as the random effect. Residuals of linear-model models were analyzed to test normality. All analyses were performed using R 2.14.0 (R Development Core Team, 2011) and the nlme package for mixed effect models. Furthermore, the diversity of the macrofauna community was analysed using rarefaction curves (Gotelli and Colwell, 2001) performed with the EstimateS 8.0 software (Colwell, 2006). To compare both sites, the rarefied taxonomic richness were plotted ("rescaled") against the number of specimens collected in order to remove the effect of sampling size on observed taxonomic richness. These rarefaction curves are considered significantly different if the 95% confidence intervals do not overlap (Gotelli and Colwell, 2001).

3. Results

3.1. Biomass production and nutrient content

Aboveground production by *C. odorata* was significantly higher (11.9 ± 2.6 Mg ha⁻¹) than *H. Diplandra* (4.2 ± 0.5 Mg ha⁻¹) with approximately a ratio of 3:1 (Table 1). A similar observation was made with roots, as biomass of *C. odorata* (1.94 ± 0.4 Mg ha⁻¹) was twice that of *H. Diplandra* (0.93 ± 0.07 Mg ha⁻¹).

Apart from carbon content, *C. odorata* fresh leaves showed significantly higher values of nutrients (Table 2). Indeed, values of nutrients in *C. odorata* leaves were as many as three times in *H. Diplandra*. As far as fine roots are concerned, C, N, K and Mg showed significantly lower values in *H. Diplandra* relative to *C. odorata* (Table 2).

3.2. Soil chemical, physical and biological properties

Table 3 gives the Anova results of log-transformed chemical and physical data from both sites. Of the variables, only SOC, total N, C:N ratio, total P, Cmin, mineral-N pool and available Mg showed significant differences between both sites. However, the marked changes concerned only N-NO₃⁻, infiltration rate, total P, NH₄⁺, SOC and total N. On the other hand, the macrofaunal community was composed of 9 taxonomic units, among which termites represent the most important proportion, that is, 78.91% and 52.27% in the savannah and the fallow, respectively (Table 4). However, only earthworms showed significant changes among the soil macrofauna community (Table 5). Fig. 3 shows significantly higher median values of SOC and total N beneath the fallow (9.42 vs. 7.66 g kg⁻¹) to the savannah (0.54 vs. 0.71 g kg⁻¹). Not surprisingly, the C:N ratio decreased significantly

Table 1

Aboveground and root biomass (Mg ha⁻¹) in savannah and fallow sites. For a given column, values with different letters are significantly different.

| | Aboveground | Fine roots | Total |
|------------------------------|-------------|--------------|-------------|
| <i>Hyparrhenia diplandra</i> | 4.2 ± 0.5a | 0.93 ± 0.07a | 5.12 ± 0.6a |
| <i>Chromolaena odorata</i> | 11.9 ± 2.6b | 1.94 ± 0.4b | 13.8 ± 2.9b |

Table 2

Nutrient content (mean \pm standard error) in leaves and fine roots of *Hyparrhenia diplandra* and *Chromolaena odorata*. Values followed by the same letters in a given column are not significantly different.

| | C (%) | N (%) | P (%) | K (%) | Ca (%) | Mg (%) | C:N ratio |
|---------------------|-----------------|------------------|------------------|-----------------|-----------------|------------------|------------------|
| Leaves | | | | | | | |
| <i>H. diplandra</i> | 51 \pm 1a | 0.06 \pm 0.04a | 0.1 \pm 0.01a | 0.6 \pm 0.1a | 0.3 \pm 0.01a | 0.2 \pm 0.02a | 72.4 \pm 13.3a |
| <i>C. odorata</i> | 50.8a | 2.2 \pm 0.4b | 0.3 \pm 0.01b | 1.8 \pm 0.2b | 1.8 \pm 0.1b | 0.6 \pm 0.05b | 28.3 \pm 8.6b |
| Fine roots | | | | | | | |
| <i>H. diplandra</i> | 48.7 \pm 1.4a | 0.54 \pm 0.1a | 0.09 \pm 0.01a | 0.3 \pm 0.08a | 0.2 \pm 0.02a | 0.1 \pm 0.01a | 100 \pm 15a |
| <i>C. odorata</i> | 54 \pm 0.2b | 0.9 \pm 0.1b | 0.07 \pm 0.00a | 1.4 \pm 0.1b | 0.2 \pm 0.01a | 0.35 \pm 0.01b | 59 \pm 4.7b |

from the savannah (14.26) to the fallow (13.25). The cumulative Cmin over 21 incubation days was significantly higher under the fallow (119.66 mg g C⁻¹) compared with the savannah (91.44 mg g C⁻¹). N-NO₃⁻ contents were significantly lower in the savannah (7.95 μ g g soil⁻¹) relative to the fallow (13.85 μ g g soil⁻¹). The same observation applies for N-NH₄⁺ content with 8.04 μ g g soil⁻¹ and 14.19 μ g g soil⁻¹ under the savannah and the fallow, respectively (Fig. 3).

The median value of infiltration rate of water beneath the fallow (1.65 cm min⁻¹) was significantly faster than the 0.20 cm min⁻¹ recorded in the savannah (Fig. 4). Looking at the evolution of the infiltration rate over time (Fig. 5), values under the fallow (2.28 \pm 0.16 to 1.22 \pm 0.11 cm min⁻¹) were far beyond that of the savannah (0.59 \pm 0.08 to 0.23 \pm 0.06 cm min⁻¹) and the discrepancy between both curves was high and constant. Moreover, the steady state in the savannah was reached 20 min after the beginning of the experiment, while it was hardly attained in the fallow over time (Fig. 5). The median value of total P hits 260.2 mg kg⁻¹ under the fallow, relative to 156 mg kg⁻¹ found beneath the savannah (Fig. 5). Median values of earthworm density and biomass between the savannah and fallow varied from 60 to 164 ind m⁻² and 5.76 to 12.85 g m⁻². As for the exchangeable Mg, the values increased from the savannah (0.63 cmolc kg⁻¹) to the fallow (1.54 cmolc kg⁻¹) like for previous variables (Fig. 6).

3.3. Diversity in the soil macrofauna community

A total of 2239 individuals belonging to 8 taxonomic units were collected in the two sites (Table 5, Appendix A). At first, the taxonomic richness in the fallow seemed higher than in the savannah, which in turn harboured more individuals (Fig. 4). However, when the number of taxonomic units was standardized to the number of individuals, the taxonomic richness was found to be similar across both sites as 95% confidence intervals largely overlapped (not shown on

Fig. 4), indicating that the positive effect of fallow on observed taxonomic units is most likely explained by a sampling effect. At plot level, earthworms and termites were the most common group accounting for 90.44% and 85.3% of total density in the savannah and fallow, respectively (Table 5). In terms of community structure, termites were the most important in density with values ranging between 52.3% (Fallow) and 78.9% (Savannah), though there were no marked changes in their density and biomass (Table 4). They were followed by earthworms, which represented 11.5% and 33% in the savannah and the fallow, respectively.

4. Discussion

4.1. Biomass production and nutrient content

In line with a rapid visual assessment of the two land covers, the biomass data demonstrates that *C. odorata*-dominated fallow is characterized by a huge amount of aboveground biomass. A similar result was found with the fine roots biomass, though the difference was less. The two main reasons likely to explain the high value of *C. odorata* biomass are (i) the establishment of a yam-field considered as the disturbance factor prior to the fallow settlement as man-modified ecosystems are known to favour the colonization of exotic weeds (Chandrasekaran and Swamy, 2002; De Rouw, 1995), and (ii) the capability of *C. odorata* to expand rapidly and provide a protective cover due to the high density of seed, the short-term persistence of the seed bank in the soil of such opened areas (Witkowski and Wilson, 2001) characterized by a forest-savannah transition area. Although up to 78 species were recorded in the fallow, the aboveground biomass was markedly made up with *C. odorata* so that it could be referred to as a *C. odorata*-based fallow. One of the possible explanations is an inhibitory effect of *C. odorata* on the growth of others plant species, due to the presence of a large amount of allelochemicals that may inhibit the growth of many plants as reported by Gill et al. (1996). Further studies assessing the impact of fallow invasion by *C. odorata* on plant or weed communities in relation to soil properties will shed light on how it interacts with other plant communities. The high values of nutrient contents (P, K, Ca, Mg) and the low value of the C:N ratio in leaves along with fine roots of *C. odorata* provide evidence of the good quality of *C. odorata*-based fallow residues relative to the shrub savannah. Similarly, it has been reported that the aboveground biomass of the legume cover crop *Mucuna pruriens*

Table 3

Anova table of general linear mixed effect models of transformed (log) soil chemical and physical variables. df: degrees of freedom, significant effects ($p < 0.05$) are given in bold.

| | df | F-values | p |
|---|----|----------|---------------|
| SOC (g kg ⁻¹) | 4 | 16.9 | 0.0147 |
| N (g kg ⁻¹) | 4 | 16.2 | 0.0157 |
| C:N | 4 | 12.2 | 0.0252 |
| pH-H ₂ O | 4 | 2.72 | 0.175 |
| MBC (mg kg soil ⁻¹) | 4 | 0.088 | 0.78 |
| Cmin (mgC-CO ₂ g org C ⁻¹) | 4 | 8.47 | 0.044 |
| NH ₄ ⁺ (μ g g soil ⁻¹) | 4 | 18.7 | 0.0124 |
| NO ₃ ⁻ (μ g g soil ⁻¹) | 4 | 191.04 | 0.0002 |
| Infiltration rate (cm min ⁻¹) | 4 | 86.97 | 0.0007 |
| Bulk density (g cm ⁻³) | 4 | 0.008 | 0.93 |
| Clay + silt (%) | 4 | 0.28 | 0.621 |
| Total P (mg kg ⁻¹) | 4 | 28.46 | 0.0059 |
| Available P (mg kg ⁻¹) | 4 | 0.72 | 0.443 |
| CEC (cmolc kg ⁻¹) | 4 | 0.0032 | 0.9576 |
| Exchangeable Ca (cmolc kg ⁻¹) | 4 | 1.34 | 0.3114 |
| Exchangeable K (cmolc kg ⁻¹) | 4 | 0.00064 | 0.981 |
| Exchangeable Mg (cmolc kg ⁻¹) | 4 | 15.64 | 0.0167 |

Table 4

Relative abundance (%) of soil macrofauna across sites.

| Taxonomic units | Savannah | Fallow |
|-------------------|----------|--------|
| Earthworms | 11.53 | 33.03 |
| Termites | 78.91 | 52.27 |
| Ants | 5.13 | 7.82 |
| Coleoptera | 0.14 | 0.20 |
| Coleoptera larvae | 2.23 | 2.92 |
| Chilopoda | 1.08 | 2.48 |
| Diplopoda | 0.00 | 0.34 |
| Arachnida | 0.37 | 0.22 |
| Diptera larvae | 0.61 | 0.72 |

Table 5

Anova table of general linear mixed effect models of transformed (log) biological data. df: degrees of freedom, significant effects ($p < 0.05$) are given in bold.

| | df | F-values | p |
|---|----|----------|--------------|
| Macrofauna density (ind m ⁻²) | 4 | 0.12 | 0.74 |
| Macrofauna biomass (g m ⁻²) | 4 | 4.27 | 0.11 |
| Earthworm density (ind m ⁻²) | 4 | 10.20 | 0.033 |
| Earthworm biomass (g m ⁻²) | 4 | 10.17 | 0.033 |
| Termite density (ind m ⁻²) | 4 | 1.33 | 0.31 |
| Termite biomass (g m ⁻²) | 4 | 0.25 | 0.64 |

contains $2.6 \pm 0.05\%$ N, $0.2 \pm 0.01\%$ P and $1.4 \pm 0.04\%$ K (Anthofer and Kroschel, 2005), indicating the potential of *C. odorata* fallows to improve soil quality. Based on nutrient content in leaves, the input of N, P, K due to the presence of *C. odorata* in the system is estimated at 26.2, 3.6 and 21.4 Mg ha⁻¹, respectively. These findings are consistent with observations about the capability of *C. odorata* fresh biomass to sequester high quantities of nutrients in South-western Nigeria (Aweto, 1981) and Northern Laos (Roder et al., 1995), to decompose and release nutrients quickly (Kammegne et al., 1999). These results revealed that *C. odorata*-based fallows produce litter of good quality and may consequently improve soil quality. They also confirmed previous observations that invasive species combine production of large aboveground and root

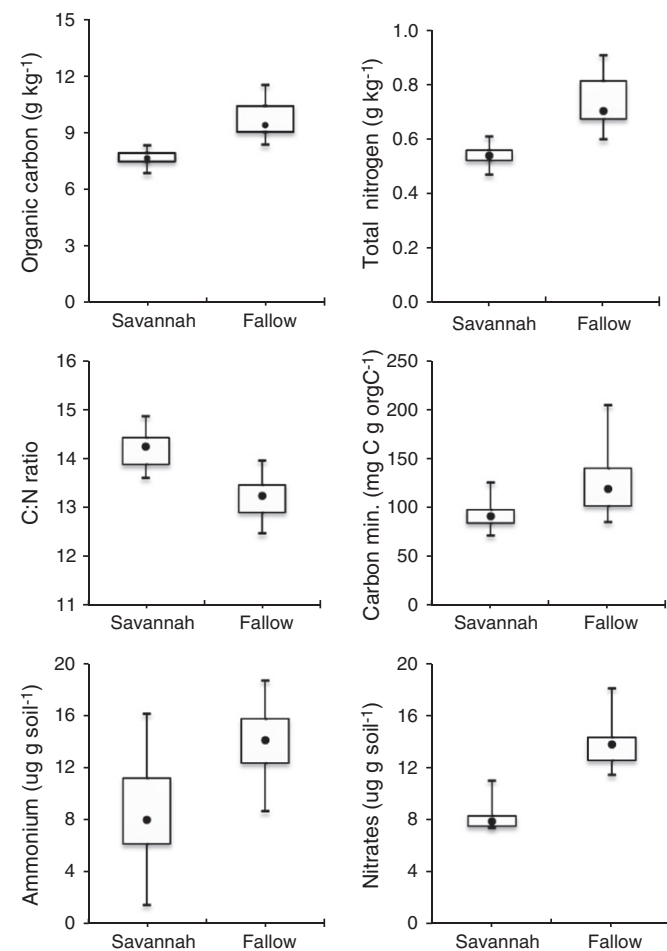


Fig. 3. Comparative distribution of soil organic carbon, total nitrogen, C:N ratio, carbon mineralized, ammonium and nitrates across the sampling sites.

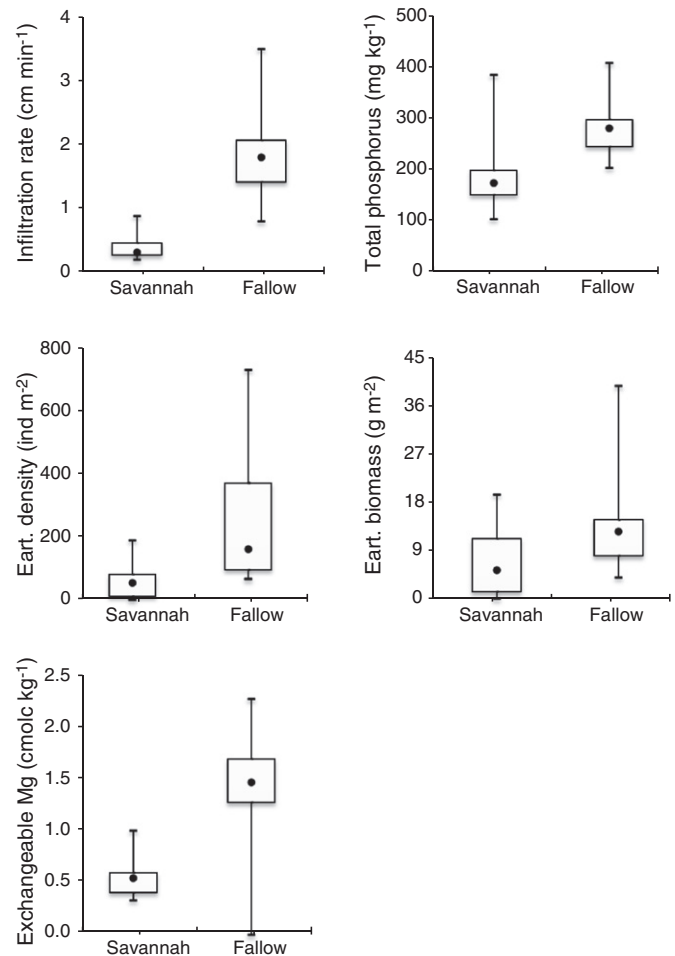


Fig. 4. Comparative distribution of water infiltration, total phosphorus, earthworm density, earthworm biomass and exchangeable magnesium in sampling sites.

biomass with N-rich residues characterized with high decomposition rate (Ehrenfeld et al., 2001; Evans et al., 2001; Koné et al., 2012a,b).

4.2. Change in soil quality under *C. odorata*-dominated fallows

In general, results showed that *C. odorata*-based fallow was associated with higher values of chemical, physical, organic matter-related soil characteristics and soil macrofauna abundance relative to the shrub savannah, suggesting the potential of this fallow to improve soil quality in humid savannahs.

4.2.1. Change in chemical and physical properties

The significant increases of SOC (+27.3%) and total N (+36.7%) under the fallow within the 0–10 cm layer revealed the potential of *C. odorata*-based fallow to build up soil organic matter as SOC and total N provide a measurement of SOM status (Goyal et al., 1999; Manjaiah et al., 2000), a key attribute of soil quality (Gregorich et al., 1994; Kibblewhite et al., 2008). As far as chemical characteristics are concerned, only total phosphorus (+56.8%) and exchangeable magnesium (+140.3%) showed a clear rise from savannah to fallow. The production of huge amount of better quality residues followed by subsequent decomposition and release of total P is common in improved and natural regrowth dominated by *C. odorata* (Kolawole et al., 2003; Koné, 2009). The increase of exchangeable Mg may be attributable to high level of Mg content in the leaf litter combined with soil

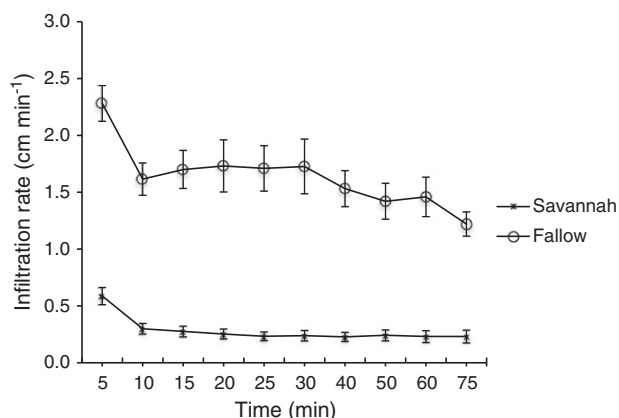


Fig. 5. Dynamic of water infiltration (mean \pm standard error) over time across the study sites.

organic carbon known to be the main factors that regulate the chemical properties in soils. These findings are in agreement with observations made by Koutika et al. (2004) revealing high values of SOC, exchangeable Mg under a 2-year-old fallow dominated by *C. odorata* in Cameroon, compared with *Pueraria phaseloides* and *Calliandra calothyrsus* fallows. Although SOC markedly changed between both sites, CEC varied slightly, likely pointing out the crucial role of clay content in the replenishment of fertility in soils with low activity clays, as reported by Kirchhof and Salako (2000).

The increase of Cmin beneath fallow is a sign of high microbial activity due to the presence of readily available organic substrates and N-rich residues as Kramer and Gleixner (2006) revealed that up to 40% of SOC is used as a substrate for soil microorganisms in agricultural soils. The recurrent input of fresh material of good quality, an essential resource of energy for soil microbes in the fallow, might have indeed stimulated the mineralisation of soil organic matter (Fontaine et al., 2003). However, the absence of increase in MBC under the fallow despite of high amounts in SOC and total N gives raise to speculations about hypothetic bacterial growth rate (Demoling et al., 2007) at the expense of fungal growth rate, as a consequence of the antagonistic relationship between both microorganisms (Meidute et al., 2008). On the

other hand, the good quality of litter and fine roots under the fallow is hypothesized to have stimulated the growth of soil nematodes (Chen et al., 2007; Ferris and Bongers, 2006), which in turn will feed on bacteria (Salinas et al., 2007) and therefore reduce the size of the microbial biomass. Microbial biomass C as a percentage of SOC was unaffected by fallow in contrast to the commonly agreed trend of increase under organic amendments and green manure systems (Wick et al., 1998; Goyal et al., 1999; Manjaiah et al., 2000; Koné et al., 2012a). As regards N min, the increased amount of mineral N-NO₃⁻ (+72.5%) and N-NH₄⁺ (+71.5%) beneath the fallow relative to the savannah is likely due to the high quality of *C. odorata* residues that decomposes rapidly and increase the pool of mineral N in the soil. Similar results were found by Evans et al. (2001) who identified change in the quantity and quality of plant residues as the mechanism responsible for exotic plant invasion consequences on soils. The process by which *C. odorata* fallow increases nutrients in the soil is unclear, though we suspect that the deep rooting system has a major role to play in the mobilization of soil mineral nutrients that are further turned into organic and then plant-available form. Investigations in nutrients uptake beneath *C. odorata* fallows will improve the understanding of mechanisms involved.

Results regarding soil physical properties indicate an increase in water infiltration rate by 88.8% in the fallow. The positive role of natural fallow, composed mainly of *C. odorata*, in improving physical characteristics under a degraded Alfisol in Nigeria has been underlined (Salako et al., 2000). Moreover, Obi (1999) has also found a significant relative increase of the water infiltration rate in 5-year-old legume cover crops compared with bare soils in southern Nigeria and attributed it to the increase of macroporosity and the decrease of microporosity. Indeed, as a deep-rooted shrub, *C. odorata* along with trees and shrubs in the fallow could have increased soil macroporosity and soil aggregation via the physical impact of roots and beneficial effect on earthworm abundance and activity, though no marked relationship was found between these invertebrates and the infiltration rate.

4.2.2. Change in the soil macrofauna community

The abundance and the biomass of soil macroinvertebrates were significantly increased under *C. odorata* fallow. In the same way, Blanchart et al. (2006) reported a rise in the abundance and biomass of soil macrofauna beneath a long term *Mucuna pruriens* fallow. Although termites were the most important group in terms of density, the lack of significance of the their density variation was likely caused by (i) their markedly clumped distribution, which certainly resulted in high variation among sampling plots, and (ii) the inappropriate sampling protocol consisting of extracting a single soil monolith (25 \times 25 \times 20 cm), that did not fit the clumped distribution. The standard protocol for rapid assessment of termites based on 100 m long transects as recommended by Jones and Eggleton (2000) could have provided better results as recently documented by Dosso et al. (2010) in the study area. The significant increase in earthworm density and biomass in *C. odorata* fallow was similar to observations made by MBoukou-Kimbasta et al. (2007) in Congolese eucalyptus plantations invaded by *C. odorata*. Similarly, the potential of this exotic fallow to regenerate earthworm populations in degraded soils was pointed out in Nigeria (Tian et al., 2000b) and Ivory Coast (Guéi and Tondoh, 2012; Tondoh et al., 2007, 2011). Recently, Koné et al. (2012a, 2012b) reported more than a threefold increase of earthworm density in *C. odorata* fallow compared to a shrub savannah in the study area. The increase of earthworm populations in *C. odorata*-based fallows is likely due to the microclimate provided by aboveground biomass along with the good quality of plant residues characterized by low lignin/N ratio (MBoukou-Kimbasta et al., 2007), fast decomposition rate (Roder et al., 1995), high content of carbon and nitrogen. The functional consequence of the increase in the earthworm community lies in the production of

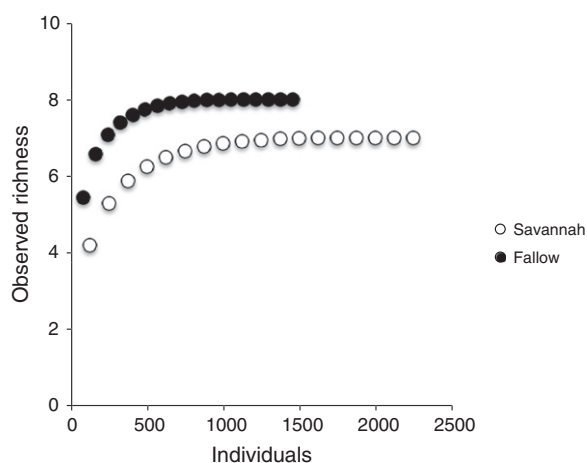


Fig. 6. Sample-based rarefaction curves standardized for number of macrofauna individuals in savannah and fallow sites. 95% confidence intervals are not shown.

stable casts, known to be active in soil organic matter storage, regulation of soil structure and physical resistance to erosion (Blanchart et al., 1997, 2006; Bossuyt et al., 2005). This assertion is confirmed by the high soil organic matter content along with the improved water infiltration capacity in the fallow. However, it is worth mentioning that if *C. odorata* has slightly modified the structure of the soil macrofauna due to the presence of diplopoda taxonomic unit, the structure of the earthworm community remained stable. Surprisingly, no invasive species such as the pantropical species *Pontoscolex corethrurus* and the African peregrine *H. africanus* were recorded.

5. Conclusion

The results of this study suggested that *C. odorata*-based fallows have the potential to improve soil quality status in humid savannah zones of Ivory Coast. Significant inputs in nitrogen, phosphorus and potassium through leaf litter, enhanced SOC and total N storage, improved water infiltration capacity and increased N-mineral pool and soil macrofauna conservation are the main beneficial consequences of *C. odorata* invasion. As a result, *C. odorata* fallows or mulch cropping systems could be one of the options to sustainably improve and maintain soil fertility in the buffer zone of the Lamto Reserve. In order to achieve this ultimate goal, the implementation of further multi-location and chronosequence trials should be undertaken to confirm current findings and also assess the impact of *C. odorata* fallows on crop yield (maize and yam), as well as the economic viability of such cropping system.

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Appendix A. Density (mean \pm SE) and biomass (mean \pm SE) of soil macrofauna under both sites

| Taxonomic units | Savannah | | Fallow | |
|-------------------|--------------------------------|------------------------------|--------------------------------|------------------------------|
| | Density (ind m ⁻²) | Biomass (g m ⁻²) | Density (ind m ⁻²) | Biomass (g m ⁻²) |
| Earthworms | 62.67 \pm 12.7 | 7.45 \pm 1.58 | 265.78 \pm 55.71 | 14.06 \pm 2.11 |
| Termites | 1854.67 \pm 794.97 | 4.73 \pm 2.10 | 882.67 \pm 310.05 | 3.69 \pm 1.64 |
| Ants | 28.00 \pm 11.45 | 0.17 \pm 0.11 | 56.67 \pm 37.46 | 0.79 \pm 0.48 |
| Coleoptera | 1.33 \pm 0.74 | 0.03 \pm 0.02 | 2.22 \pm 1.11 | 0.04 \pm 0.02 |
| Coleoptera larvae | 16.00 \pm 2.90 | 0.36 \pm 0.15 | 24.00 \pm 8.10 | 0.30 \pm 0.09 |
| Chilopoda | 5.78 \pm 2.08 | 0.04 \pm 0.01 | 21.78 \pm 4.50 | 0.15 \pm 0.03 |
| Diplopoda | – | – | 2.67 \pm 1.15 | 0.17 \pm 0.09 |
| Arachnida | 2.22 \pm 1.11 | 0.09 \pm 0.05 | 2.67 \pm 1.49 | 0.08 \pm 0.05 |
| Diptera larvae | 1.33 \pm 0.74 | 0.03 \pm 0.03 | 4.89 \pm 2.01 | 0.03 \pm 0.01 |

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