



Effects of plant diversity on plant biomass production and soil macrofauna in Amazonian pastures

Kam-Rigne Laossi^{a,*}, Sébastien Barot^a, Deurival Carvalho^b,
Thierry Desjardins^{a,b}, Patrick Lavelle^a, Marlucia Martins^c,
Danielle Mitja^{a,d}, Ana Carolina Rendeiro^c, Guillaume Rousseau^e,
Max Sarrazin^{a,b}, Elena Velasquez^a, Michel Grimaldi^a

^aUMR 137–IRD/UPMC, 32 Avenue Henri Varagnat, 93143 Bondy Cedex, France

^bUFRA, Av. Pres. Tancredo Neves 2501, Terra Firme, 66.077.530 Belém, PA, Brazil

^cMuseu Paraense Emílio Goeldi, Av. Perimetral 1901, Terra Firme, 66.077.530 Belém, PA, Brazil

^dEMBRAPA Cerrados, CP 08223, 73310-970 Planaltina, DF, Brazil

^eEMBRAPA Amazônia Oriental, Tr. Enéas Pinheiro, s/n CP 48, Marco, 66095-100 Belém, PA, Brazil

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Summary

We examined the effect of plant diversity on plant production and soil macrofauna density and diversity. Four plants species (*Arachis pintoi*, an herbaceous legume; *Brachiaria brizantha*, a perennial grass; *Leucaena leucocephala*, a legume shrub; *Solanum rugosum*, a non-legume shrub) were used in a field experiment and communities of all combinations of one, two, three or four species were established. Plant diversity neither significantly affected density and diversity of soil macrofauna nor total plant biomass, however, the biomass of specific plants was negatively affected by plant diversity. Earthworm and ant densities were significantly higher in the presence of *A. pintoi* although this plant influenced neither the density of the other group nor fauna diversity. Earthworm and diplopod densities increased significantly with shoot biomass of *A. pintoi*. Fauna diversity increased significantly with shoot biomass (specific and total). Root biomass did not affect fauna density and diversity. Our results suggest that fauna density is affected by litter quality and that it is more affected by resource quantity than quality. Our results also confirm the importance of nitrogen fixers to ecosystem function.

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*Corresponding author. Tel.: +33 1 48 02 55 01; fax: +33 1 48 02 59 70.

E-mail address: kam-rigne.laossi@bondy.ird.fr (K.-R. Laossi).

Introduction

Many studies (Wardle et al., 2004; Bardgett, 2005) have already provided evidence of the close links between vegetation and soil fauna. Indeed, through the quality and quantity of litter produced (Hooper et al., 2000) and the secretion of various types of root exudates (Lavelle et al., 1995), plants modify the abundance and diversity of organic resources and microhabitats (Scheu and Schaefer, 1998; Gastine et al., 2003b). Conversely, soil fauna plays an essential role in nutrient cycling and the dynamics of organic matter. Soil fauna, via its activity, increases decomposition which, in turn, liberates mineral nutrients thus increasing nutrient availability to plants (Lavelle, 1996; Bradford, 2002). Moreover, many soil invertebrates such as earthworms, ants and termites, play a particular role in the regulation of soil processes (Lavelle et al., 1997). Given the effect of soil fauna on soil properties and primary production, it seems important to manage soil macrofauna in order to maintain soil fertility, especially in agroecosystems (Lavelle et al., 1994, 1999). Due to the effect of plants on soil fauna, the manipulation of plant diversity presents an attractive possibility for managing soil fauna.

Plant biodiversity plays in itself a crucial role by influencing essential functions of ecosystems such as primary production, organic matter decomposition, nutrient and water cycling (Loreau, 2000; Gastine et al., 2003a; Balvanera et al., 2006). Increasing plant diversity tends to increase primary production and nutrient retention (Naeem et al., 1994; Tilman et al., 1996; Hector et al., 1999). Two mechanisms are usually invoked to explain these effects: the sampling effect and the complementarity effect (Loreau and Hector, 2001). The odds of including highly productive species in a sample increases with the number of species in the mixture. If these species dominate the plant community, primary production increases statistically with the number of species, through a sampling effect. Alternatively, if plant species use resources in a complementary way, greater plant diversity increases the efficiency of resource use by the plant community and is thus also likely to augment primary production. According to some authors, the presence of key functional groups like legumes is more important than the effect of biodiversity within functional groups (Díaz and Cabido, 2001). Again, increasing plant biodiversity may enhance the probability of having species belonging to these key groups and therefore, of increasing primary production.

The study of the relationships between above-ground (plant) and belowground (faunal) biodiversity is a newer line of research than the study of the functional consequences of plant diversity (Bardgett et al., 2005). Therefore, limited predictions have been made about these relationships and even fewer studies have been published on this subject than on the relationships between plant diversity and ecosystem functioning. A high level of specific or functional diversity of plants is likely to lead to a high diversity of litter quality. If species of soil fauna have a complementary use of the different types of litter, plant diversity may thus increase soil fauna diversity (Hooper et al., 2000). Plant diversity could also increase soil fauna diversity through an increase in microhabitat diversity. Alternatively, as particular plant functional groups may have a specific positive effect on primary production or provide a litter of a particularly good quality, some plant functional groups might increase the densities of the soil macrofauna groups that feed on their litter or that benefit from the microhabitats they provide. Conversely, a high level of soil fauna diversity may enhance the efficiency of organic matter decomposition through a synergistic interaction between organisms, which may increase nutrient availability and plant productivity (Cragg and Bardgett, 2001). Plant biomass and primary production is often supposed to have a direct bottom-up positive effect on soil fauna density that is independent of plant diversity (Chen and Wise, 1999) and diversity (Hooper et al., 2000), since organic matter is the essential resource for the soil trophic network.

To our knowledge, no studies have investigated the relationship between aboveground diversity, plant biomass and belowground diversity tropical ecosystems. In our experiment, we manipulated four plant species belonging to four functional groups so that plant diversity differed between one and four in 100 m² plots. Specifically, we aimed at assessing (1) the effect of plant diversity on plant biomass and (2) the effect of plant diversity and biomass on soil macrofauna in an Amazonian pasture. Specifically, we tested three hypotheses: (1) an increase in plant diversity enhances the amount of plant biomass produced, (2) plant diversity increases macrofauna diversity through the diversity of produced resources and (3) plant biomass has a positive effect on the diversity and density of soil macrofauna independent of plant diversity. The essential objective of this study is thus theoretical and aims at improving our understanding of below- and above-ground interactions.

Materials and methods

Study site

The study was conducted in the Brazilian state of Pará, in Benfica (5°16'S; 49°50'W) on the pioneer front near the town of Marabá. The landscape is fragmented and consists of a network of 50 m high hillocks mainly covered by forests and pastures. The climate is characterized by a mean annual temperature of 26 °C and about 1800 mm of annual rainfall, with a marked dry season from June to November. Clayey Ferralsols (ISSS Working Group R.B. 1998) are the dominant soils (pH 5, carbon content 2.7%, C/N ratio 15).

Experimental design

The experiment was established on December 2002 in three pastures (hereafter pastures A, B and C) that were sown with *Brachiaria brizantha*. Pastures A, B and C were sown 6, 7 and 8 years ago, respectively. All pastures had similar topographic positions and soil characteristics (depth, texture, pH, organic matter content). However, the three pastures were located at different distances from the nearest patch of forest with B being the closest, and A the furthest. We used four plant species belonging to four different functional groups: a leguminous ligneous plant, *Leucaena leucocephala* (it produces a rather dense leaf biomass at about 1.50 m above the ground); a leguminous herbaceous plant *Arachis pintoi* (it produces a very dense leaf cover just above the ground); an African grass widely introduced as forage, *B. brizantha* (*B. brizantha* tufts totally cover the ground and reach a height of 1–1.5 m); and a native ligneous plant, *Solanum rugosum* (it produces a small leaf biomass at the same height as *L. leucocephala* but hardly covers the ground). Seeds of the two legumes and *S. rugosum* were sown while *B. brizantha* was already established. One-half, two-thirds and three-quarters of *B. brizantha* tufts were removed from the plots in which the plant was associated with one, two or three other plants, respectively. Weeds were frequently removed and plots were maintained for two-and-a-half years. To test both the respective influence of each plant species and interactions between them, all combinations of one, two, three or four species were planted in an enclosure deprived of cattle. The enclosure also included a control treatment, which consisted of unweeded *B. brizantha* plots. True control plots were outside the enclosure (i.e., plots of *B. brizantha* – grazed pasture). The experimen-

tal design had thus 17 treatments with different combinations of one, two, three or four species and two controls. We used two controls consisting of *B. brizantha* plots but one of them was in the enclosure and was thus protected from grazing while the other was outside the enclosure and was grazed. Each treatment was repeated three times in each of the three selected pastures. Treatments were randomly assigned to plots within a pasture. Plot size was 10 m × 10 m. Plots were separated by 2 m wide corridors.

At the end of the experiment, two sub-plots of 1 m² were randomly chosen in each plot. In these sub-plots, all aboveground biomass was harvested and sorted according to species. Samples were dried (48 h at 60 °C) and weighed. For the ligneous plants (*S. rugosum* and *L. leucocephala*), we separated leaves from ligneous material. Root biomass was assessed by extracting two soil cores per plot (7.3 cm diameter × 10 cm depth). Roots were isolated by wet sieving with a 500 µm mesh and dried for 48 h at 60 °C, and weighed. The sampling of macrofauna was carried out according to the methodology recommended by the Tropical Soil Biology and Fertility Programme (Anderson and Ingram, 1993). It was based on the excavation of soil monoliths of 25 × 25 × 30 cm in each of the 1 m² sub-plots. The macrofauna was hand-sorted in the field. Invertebrates were identified to taxonomic groups (i.e., earthworms, ants, termites, Isopoda, Coleoptera, Arachnida, Diplopoda, Orthoptera) and counted. Previous studies showed that the classification of macrofauna in broad taxonomic groups is relevant (Benito et al., 2004; Brown et al., 2004; Decaëns et al., 2004): significant effects of land uses have been observed on the density or diversity of these broad groups. Two 25 × 25 × 30 cm blocks of soil per experimental plot are not sufficient to assess precisely the species diversity; however, numbers of individuals in broad taxonomic groups and the number of represented broad taxonomic groups should be robust indicators of the effect of vegetation on soil fauna. Here, we only present results from the 0 to 10 cm layer because of the scarcity of macrofauna below 10 cm.

Statistical analysis

We tested simple effects and interactions with ANOVA and ANCOVA using the SAS GLM procedure (sum of squares type III, SS3) (SAS, 1990). The ANCOVA was used to test, with the same model, the effects on fauna density and diversity of the biomass of different plant (covariate). These effects were tested on soil macrofauna density and diversity (i.e., number of

groups), root biomass and total biomass. Each model included a pasture effect to take into account the non-independence of plots established in the same pasture and, when possible, the interactions between the pasture and the main effects. To determine the direction of significant effects, we used multiple comparison tests based of least-square means (hereafter LS means, LS means SAS statement). For simplicity and to avoid redundant tables, only the results of these LS means analyses are presented.

Linear model residuals were inspected for normality and homogeneity of variance and data were transformed where required (we have used logarithmic transformation for termite, ant and diplopod densities, and square-root transformation for earthworm density). Throughout the article, "treatment" refers to the combination of species in plots while "diversity" refers to the effective number of species in plots at the end of our experiment (we were not able to maintain a species in some treatments).

Finally, some authors recommend the use of sum of squares type I (SS1) when analysing biodiversity data (Schmid et al., 2002). They argue that SS1 is more likely to demonstrate significant effects of biodiversity. Therefore, we checked that our statistical results remained unchanged using SS1 instead of SS3 and especially that the use of SS1, in our case, did not lead to more significant effects of plant diversity on density and diversity of fauna. We thus only presented SS3 statistics.

The following abbreviations are used in the text and tables to differentiate biomass-related terms: Bm-A, *A. pintoi* shoot biomass; Bm-L, *L. leucocephala* shoot biomass; Bm-S, *S. rugosum* shoot biomass; Bm-B, *B. brizantha* shoot biomass; Shoot-Bm, shoot biomass; Root-Bm, root biomass; Total-Bm, total biomass (i.e., Shoot-Bm+Root-Bm).

Results

Plant biomass

Shoot-Bm ($r^2 = 0.74$), Root-Bm ($r^2 = 0.72$) and Total-Bm ($r^2 = 0.66$) were significantly affected by

treatments (Table 1). In general, the highest shoot biomass was found in treatments including *L. leucocephala* (Figure 1). The highest shoot biomass was more than three times higher than the lowest value (Figure 1). Our LS means results (detailed results not presented) confirmed that the highest total and shoot biomass was observed for the treatment with the two legumes. LS means results indicated that treatments including *B. brizantha* generally led to higher root biomass, whereas the monoculture of *S. rugosum* had the lowest root biomass (detailed results not presented). The highest root biomass was more than ten times higher than the lowest (Figure 2).

Bm-A ($r^2 = 0.38$), Bm-B ($r^2 = 0.25$) and Bm-L ($r^2 = 0.38$) were significantly affected by plant diversity while Shoot-Bm, Root-Bm and Total-Bm were not (Table 2). Shoot biomass (in absolute values) decreased significantly with increasing plant diversity as indicated by our LS means results (detailed results not presented).

Soil macrofauna

Effect of treatments

Only earthworm, termite and ant densities were significantly affected by treatments (respectively, $P < 0.001$ and $r^2 = 0.79$; $P = 0.009$ and $r^2 = 0.63$; $P = 0.03$ and $r^2 = 0.63$). A significant pasture effect was also found for earthworms, termites and ants (respectively, $P < 0.001$, $P < 0.01$ and $P < 0.03$). Their densities were higher in the 7-year-old pasture (B) according to our LS means results. The treatment \times pasture interaction was not significant ($P > 0.05$). Generally, the highest densities of these groups were found in treatments including *A. pintoi* as indicated by our LS means results (detailed results not presented). The maximum density of earthworms was found in the treatment with *A. pintoi* and *S. rugosum*, and the minimum density was found in *B. brizantha* and *L. leucocephala* treatments. The highest earthworm density (25.67 individuals m^{-2}) was four times that of the lowest (6.17 individuals m^{-2} ; Figure 3).

Table 1. ANOVA table of *F*-value on the effect of treatments, blocks (pastures) and their interactions on plant biomasses.

	d.f.	Total biomass	Shoot biomass	Root biomass
Treatment	16	3.22**	5.53***	6.07***
Pasture	2	0.48 NS	0.30 NS	0.61 NS
Treatment \times pasture	32	1.35 NS	1.54 NS	0.97 NS
r^2		0.66	0.74	0.72

Asterisks (*), (**) and (***) significant at 5%, 1% and 1‰ level, respectively. Total d.f. = 100.

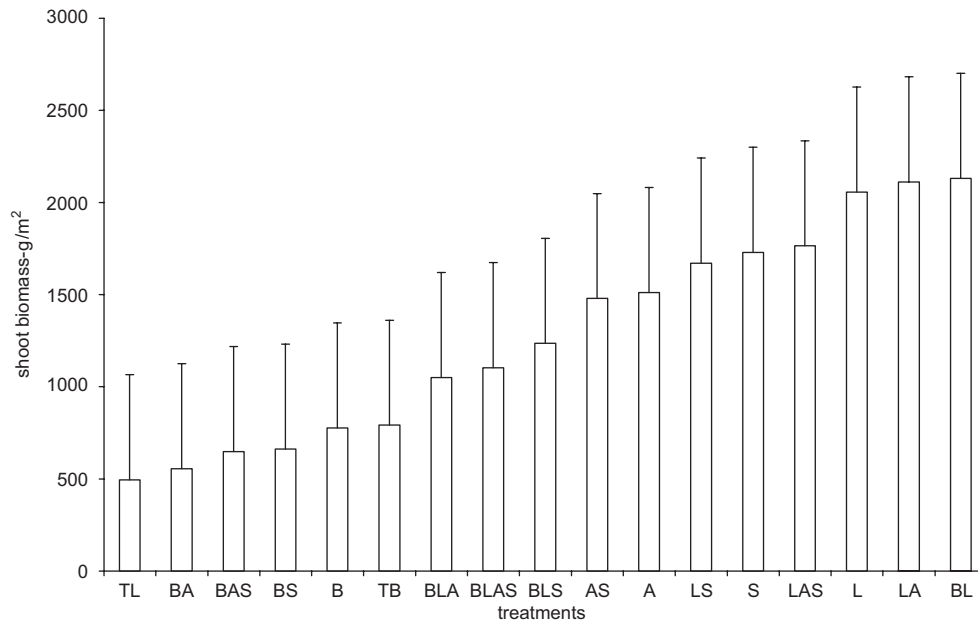


Figure 1. Average total biomass produced by treatment at the end of the experiment expressed in g of dry weight m⁻² (A, *A. pintoi*; B, *B. brizantha*; L, *L. Leucocephala*; S, *S. rugosum*; TL, grazed control; TB, non-grazed control).

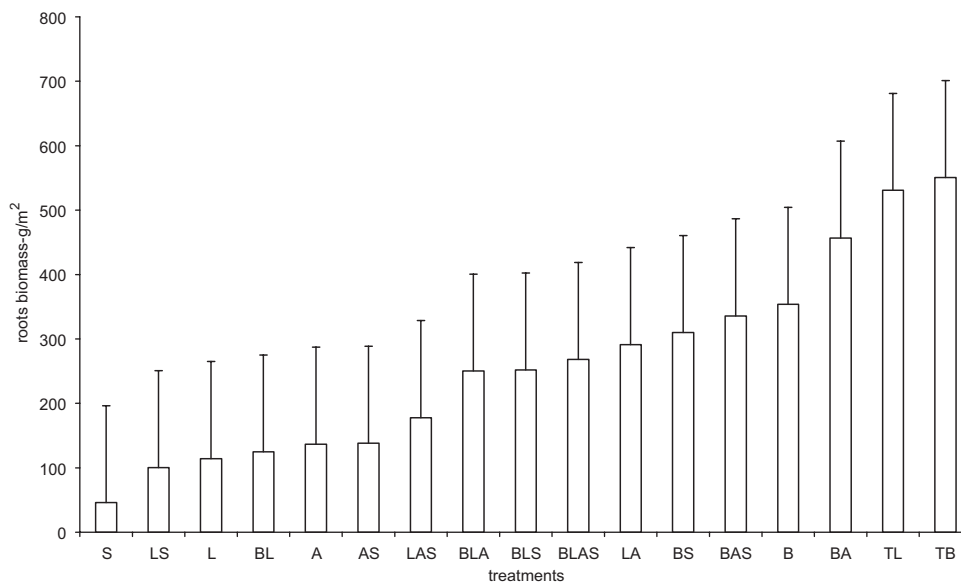


Figure 2. Effects of treatment on roots biomass expressed in g of dry weight m⁻² at the end of the experiment (A, *A. pintoi*; B, *B. brizantha*; L, *L. Leucocephala*; S, *S. rugosum*; TL, grazed control; TB, non-grazed control).

Table 2. ANOVA table of *F*-value on the effect of plant diversity, block (pasture) and their interaction on plant biomasses.

	d.f.	Bm-A	Bm-S	Bm-B	Bm-L	Total-Bm	Shoot-Bm	Root-Bm (0–10 cm)
Diversity	2	3.97***	0.35 NS	6.3**	4.90***	0.19 NS	0.66 NS	0.20 NS
Pasture	2	0.38 NS	0.18 NS	0.51 NS	0.23 NS	0.85 NS	0.16 NS	1.38 NS
Diversity × pasture	4	1.17 NS	0.37 NS	0.74 NS	1.81 NS	0.64 NS	0.58 NS	0.32 NS
<i>r</i> ²		0.38	0.19	0.25	0.38	0.07	0.06	0.03

Asterisks (*), (**) and (***) significant at 5%, 1% and 1‰ level, respectively. Total d.f. = 101.

Effect of single plant species and plant diversity

The presence of *S. rugosum*, *L. leucocephala* and *B. brizantha* had no significant effect on soil macrofauna density and diversity. Earthworm and ant densities were significantly affected by the presence of *A. pintoii* (Table 4), although this plant did not influence significantly the density of the other groups ($P = 0.74$ for isopods, $P = 0.32$ for diplopods, $P = 0.95$ for chilopods, $P = 0.28$ for arachnids, $P = 0.99$ for Coleoptera and $P = 0.24$ for Orthoptera) and fauna diversity ($P = 0.36$). Ant ($r^2 = 0.40$) and earthworm ($r^2 = 0.48$) densities were higher in the presence of the herbaceous legume (*A. pintoii*) according to LS means results (60 earthworms m^{-2} in presence of *A. pintoii* and 12.74 earthworms m^{-2} in its absence; 32.67 ants m^{-2} in presence of *A. pintoii* and 10.72 ants m^{-2} in absence of *A. pintoii*).

Fauna density and diversity (number of groups) did not respond to plant diversity (Table 3).

Effect of plant biomass

Large saprotroph (earthworms and diplopods) densities were significantly affected by Bm-A while

Bm-S, Bm-L and Bm-B did not affect fauna density (Table 5). Bm-A had a positive effect on densities of these two groups. Fauna diversity was significantly affected by Bm-A ($P < 0.01$), Bm-S ($P = 0.02$), Bm-L ($P < 0.01$), Bm-B ($P = 0.01$; multiple regression model, $r^2 = 0.41$) and by Total-Bm (simple regression, $P = 0.001$, $r^2 = 0.47$). Neither pasture effect nor the interaction between plant biomass and pasture ($P > 0.05$) had a significant effect on fauna diversity. Fauna diversity increased significantly with shoot biomass (specific and total) as shown by estimates of regression coefficients (0.0018 for Total-Bm, 0.0019 for Bm-A, 0.002 for Bm-B, 0.0009 for Bm-S and 0.001 for Bm-L). Furthermore, there was no significant effect of Shoot-Bm on densities, and none of Total-Bm on fauna density and diversity (Table 6).

Pasture effects

The pasture treatment significantly affected earthworm density (Table 3, $P < 0.001$ and $r^2 = 0.27$; Table 4, $P = 0.04$ and $r^2 = 0.48$) in models testing for the effects of plant diversity and plant species presence, respectively. Ant (Table 4,

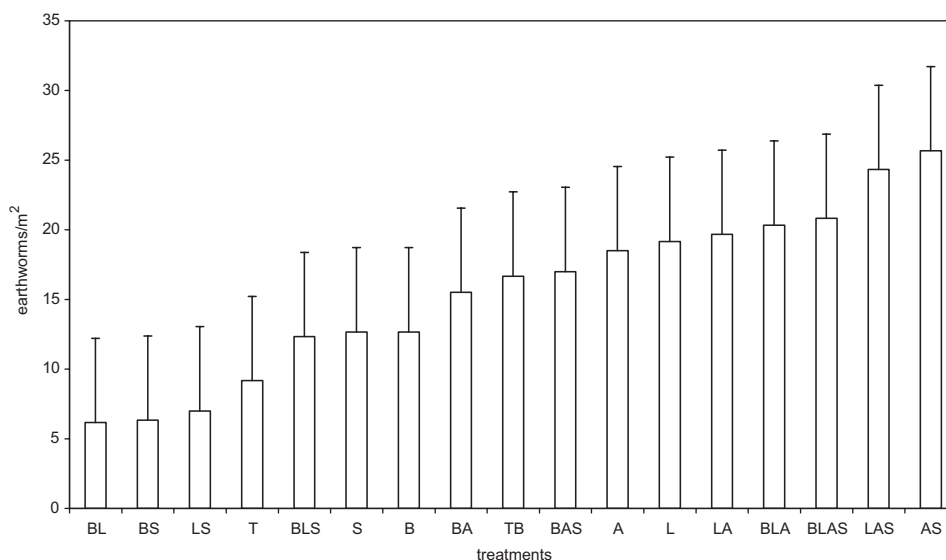


Figure 3. Density of earthworms m^{-2} for each applied treatment.

Table 3. ANOVA table of F -value on the effect of plant diversity, pasture (block) and their interaction on fauna diversity and density of macrofauna groups.

	d.f.	Earthworms	Termites	Ants	Diplopods	Fauna diversity
Diversity	2	1.28 NS	0.31 NS	0.36 NS	0.18 NS	0.43 NS
Pasture	2	9.79***	3.27**	0.22 NS	1.47 NS	0.53 NS
Pasture \times diversity	4	1.08 NS	0.76 NS	1.22 NS	1.89 NS	0.16 NS
r^2		0.27	0.16	0.05	0.08	

Asterisks (*), (**) and (***) significant at 5%, 1% and 1‰ level, respectively. Total d.f. = 101.

$P = 0.02$ and $r^2 = 0.40$) and Diplopoda densities (Table 4, $P = 0.04$ and $r^2 = 0.36$) were also significantly affected in the model testing for the effect of plant species presence. The pasture treatment affected termite densities (Table 3, $P < 0.01$ and $r^2 = 0.16$; Table 4, $P = 0.005$ and $r^2 = 0.30$; and Table 6, $P = 0.02$ and $r^2 = 0.20$) in models testing for the effects of plant diversity, plant species presence and Total-Bm on soil fauna (Tables 3, 4 and 6). When this pasture effect occurred, densities of these groups were higher in the 7-year-old pasture (B) than in other treatments. Earthworm density was significantly affected by the Bm-A \times pasture and Shoot-Bm \times pasture interaction (respectively, Table 5, $P < 0.01$ and $r^2 = 0.38$; Table 6, $P = 0.02$ and $r^2 = 0.32$). In the two cases, according to estimates of the regression coefficient (detailed results not presented), biomass effects on earthworm densities were stronger in the 7-year-old pasture (B) than in other treatments.

Discussion

Contrary to our first hypothesis, plant biomass (Total-Bm, Shoot-Bm and Root-Bm) did not increase (in absolute values) with increasing plant diversity. Moreover, plant diversity had a significant negative effect on specific shoot biomass while legumes had a positive effect on shoot and total biomass. Our second hypothesis was also invalidated, since plant diversity did not influence macrofauna diversity. However, our third hypothesis, that plant biomass has positive effects on soil macrofauna diversity and density, was confirmed.

Plant biomass

We found a significant treatment effect on Total-Bm, Root-Bm and Shoot-Bm. Legumes had a positive effect on Shoot-Bm and Total-Bm while the grass had a positive effect on Root-Bm.

Table 4. ANOVA table of F -value on the effect of species presence, pastures and their interaction on fauna density and diversity.

	d.f.	Earthworms	Termites	Ants	Diplopods
Pr-A	2	4.88**	0.89 NS	3.97**	1.87 NS
Pr-L	2	0.50 NS	0.93 NS	0.09 NS	1.71 NS
Pr-S	2	0.55 NS	0.28 NS	2.82 NS	1.72 NS
Pr-B	2	0.34 NS	1.99 NS	1.83 NS	2.35 NS
Pasture	2	3.34 [†]	5.76***	3.5 [†]	3.76 [†]
Pasture \times Pr-A	3	1.13 NS	1.06 NS	1.44 NS	0.55 NS
Pasture \times Pr-S	3	2.10 NS	1.46 NS	2.92 NS	2.79 NS
Pasture \times Pr-B	3	2.25 NS	1.29 NS	4.46 NS	0.21 NS
Pasture \times Pr-L	3	1.90 NS	0.11 NS	0.51 NS	0.98 NS
r^2		0.48	0.30	0.40	0.36

Pr-A, real presence of *A. pintoii*; Pr-B, real presence of *B. brizantha*; Pr-L, real presence of *L. leucocephala* and Pr-S, real presence of *S. rugosum*). Asterisks ([†]), (**) and (***) significant at 5%, 1% and 1‰ level, respectively. Total d.f. = 101.

Table 5. ANCOVA table of F -value testing for the effects of specific shoot biomasses block (pastures) and their interaction on fauna density.

	d.f.	Earthworms	Termites	Ants	Diplopods
Bm-A	1	5.07 [†]	0.07 NS	2.47 NS	4.97 [†]
Bm-S	1	1.05 NS	0.7 NS	0.26 NS	2.70 NS
Bm-L	1	0.14 NS	2.87 NS	0.47 NS	1.67 NS
Bm-B	1	0.22 NS	0.66 NS	2.47 NS	0.59 NS
Pasture	2	0.77 NS	0.91 NS	1.15 NS	1.82 NS
Pasture \times Bm-A	2	5.55**	0.56 NS	1.96 NS	2.83 NS
Pasture \times Bm-S	2	0.55 NS	1.14 NS	0.34 NS	1.16 NS
Pasture \times Bm-B	2	2.84 NS	1.14 NS	1.07 NS	0.75 NS
Pasture \times Bm-L	2	0.83 NS	0.29 NS	1.55 NS	1.42 NS
r^2		0.38	0.18	0.21	0.31

Asterisks ([†]), (**) and (***) significant at 5%, 1% and 1‰ level, respectively. Total d.f. = 100.

Table 6. ANCOVA table of *F*-value testing for the effects of total root and shoot biomasses block (pastures) and their interaction on fauna density and biodiversity.

	d.f.	Earthworms	Termites	Ants	Diplopods	Fauna diversity
Total root biomass	1	0.01 NS	0.13 NS	0.05 NS	1.69 NS	3.09 NS
Total shoot biomass	1	0.06 NS	0.09 NS	0.06 NS	0.66 NS	14.11***
Pasture	2	0.96 NS	0.59 NS	0.05 NS	1.35 NS	1.42 NS
Pasture × total root biomass	2	0.91 NS	0.60 NS	0.79 NS	0.32 NS	2.22 NS
Pasture × total shoot biomass	2	6.67*	0.53 NS	0.30 NS	0.30 NS	0.33 NS
<i>r</i> ²		0.32	0.20	0.18	0.24	0.47

Asterisks (*), (**) and (***) significant at 5%, 1% and 1‰ level, respectively. Total d.f. = 100.

This positive effect of legumes on Total-Bm and Shoot-Bm was due to the accumulation of wood in the case of *L. leucocephala* and to the production of a thick and continuous herbaceous cover by *A. pintoii* (Perin et al., 2003). These findings are supported by the fact that the herbaceous legume produced the highest leaf biomass (data not presented). Furthermore, legumes are nitrogen fixers and should not be limited by nitrogen as *B. brizantha* and *S. rugosum*. Nitrogen fixation contributed to their biomass production, since their built-in “fertilizing effect” (Huston et al., 2000) allowed the legumes to accumulate larger biomass than the resident perennial grass. There are two possible explanations for the higher Root-Bm found in treatments with *B. brizantha*. First, unlike nitrogen fixers, this plant needs to produce more roots for mineral nitrogen uptake. Second, *Brachiaria* plants were sown some years before the other plants when the pasture was first planted, and might consequently have had more time than the other species to develop their root system.

We found no plant diversity effect on Total-Bm, Shoot-Bm and Root-Bm. These results are consistent with several previous studies (Hooper and Vitousek, 1997; Spehn et al., 2000b; Hedlund et al., 2003; Gastine et al., 2003b). In our experiment, as observed by Hooper and Vitousek (1997), differences between treatments were due much more to species composition (identity of the species) than richness. Diversity had a significant negative effect on the shoot biomass of all plants (in absolute value). This is a clear effect of competition between the four species and suggests that in our experiment, competition between plants was more important than complementary resource use. This result also indicates that plant species were limited by the same resources. Water, light and soil nutrients such as phosphorus are likely to be limiting plant growth in this system. Nitrogen could also be limiting but this is less likely in treatments with *A. pintoii* or *L. leucocephala*.

Effects of plants on soil macrofauna

In our study, only the density of ants, earthworms and termites was significantly affected by treatments (combination of plant species). Moreover, the presence of *A. pintoii* significantly increased the density of ants and earthworms. This suggests that earthworms and ants are more sensitive to litter quality in our experiment than other groups. Our result is consistent with some published results (Wardle and Lavelle, 1997; Spehn et al., 2000b; Gastine et al., 2003b; Blanchart et al., 2006; Sileshi and Mafongoya, 2007a,b) which showed that earthworm density responds positively to legume litter. On the other hand, the effect of *A. pintoii* could also partially be due to its high production of organic matter. This hypothesis is supported by the fact that earthworms and diplopods responded positively to the shoot biomass of *A. pintoii* (Bm-A). This positive effect can also be explained by the fact that *A. pintoii* produced more leaf biomass and thus provided, at least in the short term, more organic matter to the soil (higher biomass turnover) than the ligneous legume. *A. pintoii* might also provide a better habitat for soil organisms with its complete soil cover (Perin et al., 2003).

Fauna density responded only to Bm-A and the presence of *A. pintoii* but did not respond to Total-Bm, the biomass and the presence of other plant species. This indicates that fauna density is more sensitive to the amount of a resource of high nutritive quality such as legume leaves which are nitrogen rich (Scherer-Lorenzen, 1999). Our results are consistent with those of Gastine et al. (2003b) and Salamon et al. (2004) who showed that earthworm and collembolan diversities, respectively, increased significantly in the presence of legumes. However, ants which responded positively to the presence of this legume did not increase with legume biomass. This suggests that while they benefited from the habitat provided by *A. pintoii*,

they did not use the organic matter it provided as a food source. Nevertheless, it is not possible in our study to distinguish the effect of litter quality and quantity on the density of soil macrofauna since treatments with *A. pintoi* had both the highest plant biomass and high quality litter. To our knowledge, no study to date has disentangled entirely these two possible effects at the spatial scale of our study.

Our study found, as many others have (Gastine et al., 2003b; Salamon et al., 2004; Wardle et al., 2006), that soil fauna diversity did not respond to plant diversity. This contradicts our prediction that high levels of plant diversity lead to high levels of resource diversity which should favour high fauna diversity. Our results suggest instead, as Wardle et al. (2006) have explained, that many soil fauna species are generalists in terms of feeding and habitat preference and may, therefore, be relatively unresponsive to subtle differences in resource quality. The literature in general offers contradictory results about the food preference of detritivores. Tiunov and Scheu (2004) showed that detritivores are limited by carbon availability, while research by Martin and Lavelle (1992) indicated that nitrogen availability is more important. It is not even clear which fraction of soil organic matter is assimilated by the different earthworm ecological groups (see, for example, Briones et al., 2005). Until more questions are answered about the food preference of detritivores, it will be difficult to predict whether or not plant diversity should affect soil macrofauna diversity.

We found a positive effect of total shoot biomass and all plant specific biomass on soil macrofauna diversity. This result supports the assertion that plants may affect belowground diversity through the quantity rather than the diversity of organic matter produced. The mechanism through which plant biomass or productivity could affect soil macrofauna diversity, however, is not clear. Generally speaking, there is no consensus about the relationship between resource availability and diversity of consumers. In plants, diversity is directly linked to their capacity to coexist, which depends on competition intensity that might increase or decrease with increasing soil fertility (Pärtel and Zobel, 2007). The same processes are probably involved in the relationship between soil fauna diversity and the availability of organic matter but this line of research has hardly been explored. It would be important to determine whether resource quantity increases or decreases the level of competition between groups of soil fauna.

There is an apparent contradiction between the significant positive effects of plant biomass on fauna diversity and the limited effects of plant biomass on fauna density in this study (only *A. pintoi* had significant effects on large saprotrophs while no effects of total shoot and root biomass on fauna density were found). We can propose three complementary explanations: first, an augmentation in plant production could decrease the competition between faunal groups without decreasing competition within these groups. This is possible but the underlying mechanisms remain to be determined. Second, the limited plant biomass effect on macrofauna densities could be due to a weak correlation in our experiment between plant biomass and production of plant litter. This could be due to the use of two ligneous plants and because the experiment only lasted two-and-a-half years. Spehn et al. (2000a) showed that plant biomass significantly affected soil fauna density. However, this effect of plant biomass was directly related to plant diversity, since in their study a decline in plant diversity resulted in decreasing plant biomass production. Other studies, emphasizing the positive effect of an increase of the litter quantity on soil macrofauna, directly manipulated the litter (Chen and Wise, 1999; Mboukou-Kimbatsa et al., 2007; Sileshi and Mafongoya, 2007b). One other possible explanation of our results is that plant biomass could temporarily increase fauna diversity thereby enhancing the recruitment of individuals from many groups of soil fauna that move randomly in the pastures. Most of the species studied would not reproduce more rapidly in our experimental plots, which would explain the small effect of plant biomass on macrofauna density. This problem of interpretation emphasizes the current lack of information on the distribution, movements and dynamics of soil fauna taxa at the stand and landscape scale. For example, the size of our plots was obviously sufficient to obtain a response from fauna. However, we are not able to predict how this response would have changed with smaller or larger plots or with plots closer or farther from forest patches. This is partially due to the fact that we do not know whether taxa that responded to our experimental design were already present in pastures but at lower densities or whether they emigrated from other parts of the vegetation mosaic.

In the present study, most statistical analyses showed a significant effect of the pasture. This suggests first, that soil fauna subtly depended on the land use history of plots and that even the small differences between our pastures were probably influential. Second, we found the highest density of

earthworms, ants, diplopods and termites in the 7-year-old pasture. This result could be explained by the fact that this pasture was the closest to a forest and was surrounded by a stand of palm trees, which could facilitate fauna recruitment. Again, more knowledge about soil fauna horizontal mobility would be necessary to confirm this interpretation. While these are the most evident factors that could explain differences between pastures, small differences in texture or nutrient content could also be involved.

Conclusion

Our results confirm observations from studies on the effects of plant diversity on soil macrofauna in temperate ecosystems. No effect of plant diversity was found; however, plant biomass showed a strong effect on soil fauna. This finding of a positive effect of plant biomass on macrofauna diversity is new and remains to be confirmed by other studies. We lack information about feeding preference, movements of soil fauna and competition between and within groups of soil fauna. Such information is primordial to the interpretation of our results and to make prediction on the interactions between plant diversity and soil fauna.

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