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Quantity and quality of organic inputs from coppicing leguminous trees influence abundance of soil macrofauna in maize crops in eastern Zambia

G. Sileshi · P. L. Mafongoya

Abstract Soil invertebrates are the major determinants of soil processes such as organic matter decomposition and nutrient cycling. However, the effect of quantity and quality of organic inputs on soil biota has not been studied in agroforestry systems in southern Africa. Variations in soil macrofauna abundance under maize grown in fallows of *Gliricidia sepium*, *Acacia anguistissima*, *Leucaena collinsii*, *Leucaena diversifolia*, *Leucaena esculenta*, *Leucaena pallida*, *Senna siamea*, *Calliandra calothyrsus* and monoculture maize were assessed at three sites with contrasting agro-ecological conditions in eastern Zambia. It was hypothesised that spatial variations in soil macrofauna abundance under maize crops are mediated by heterogeneity in the quality and quantity of organic inputs produced by these legumes. The relationships between the abundance of macrofauna groups and litter, leaf, stump re-sprout and recycled biomass, stump survival and the quality index lignin (L)+polyphenol (P) to nitrogen (N) ratio were assessed using generalised linear models assuming spatial randomness (Poisson distribution) and aggregation (negative binomial distribution). Earthworms, beetles and millipedes showed spatial aggregation, which was partly explained by the heterogeneity in organic resource quantity and quality. Earthworms and beetles were more abundant under legumes that produced high quantities of biomass with low (L + P) to N ratios and species that have high stump survival after coppicing. Millipedes were favoured by species which produced high quantities of biomass with high (L + P) to N ratios. Although ants and termites showed spatial aggregation, their distributions were not influenced by the quantity or quality of biomass produced by the legumes. Centipedes and Arachnida showed spatial randomness, and their distribution was not influenced by any of the organic quality and quantity variables.

Keywords Agroforestry · Litter quality · Spatial dispersion

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Introduction

Legume improved fallows have been widely promoted as low-input technologies suitable for soil fertility improvement and increasing the yields of maize, the staple crop, in smallholder agriculture in southern Africa (Sanchez 2002; Mafongoya et al. 2006). Fast-growing leguminous species that produce large quantities of biomass are selected for use in improved fallows (Mafongoya et al. 1998a,b; 2006). However, these legumes differ in the quantity of organic inputs they produce and their rate of nutrient release (Mafongoya et al. 1998a,b). The nitrogen (N), polyphenol (P), lignin (L) and condensed tannin (CT) content of the litter regulate decomposition and nutrient release (Mafongoya et al. 1998a,b).

Most of the studies in agroforestry in southern Africa have concentrated on the effect of legume improved fallows on maize yield, changes in chemical properties such as soil

organic matter content (Barrios et al. 1997), nitrogen mineralization and physical properties (Mafongoya et al. 1998a,b; Chirwa et al. 2004). Whilst soil invertebrates are the major determinants of soil processes such as organic matter decomposition and nutrient cycling (Lavelle et al. 2003), the potential for manipulating the beneficial soil animals has rarely been considered in designing agroforestry practices in southern Africa. Legumes used in improved fallows differ in their impacts on the diversity and abundance of soil macrofauna (Sileshi and Mafongoya 2006; Sileshi et al. 2005). Little attention has been paid to monitoring the effects of exotic legume species on the soil biota. Sileshi and Mafongoya (2006) indicated the need for detailed studies on the effect of the quantity and quality of organic inputs produced by agroforestry species on soil biota to develop recommendations on species selection and management. It was hypothesised that spatial variations in soil macrofaunal abundance under maize crops are mediated by heterogeneity in the quality and quantity of organic inputs produced by the exotic legumes. Therefore, the objective of this study was to quantify the variations in macrofauna abundance in relation to the quantity and quality of organic inputs from leguminous species across varying agro-ecological conditions.

Materials and methods

Study sites

The study was conducted at three sites with contrasting agro-ecologies in the Eastern Province of Zambia (10–15° South and 30–33° East). The sites were Msekera and Kalunga in Chipata district located in the Plateaux, and Masumba in Mambwe district located in the Luangwa Valley. The climate across the study sites is subtropical with three distinct seasons: the warm rainy season (November–April), the cool–dry winter (May–August) and the hot–dry season (September–October). The rainfall pattern is unimodal with approximately 85% of the rain falling during December–March. The growing season starts in November and lasts between 135 and 155 days.

The experimental site at Msekera was located at Msekera Research Station (13°39′S, 32°34′ E) at an altitude of 1,025 m and received 832–1,402 mm rainfall annually during the experimental period (2001–2004). The site has a relatively fertile soil (loamy ferric luvisols). The experimental site at Kalunga Farmers' Training Centre was located at an altitude of 1,061 m with a cooler climate and received 1,174–1,661 mm rainfall during the experimental period. This site had an infertile soil consisting of ferric luvisols. The experiment at Masumba was located at Mambwe Farmers' Training Centre at an altitude of 490 m

with relatively higher temperature and lower rainfall (828–1,010 mm). The soil at this site is a fertile alluvial deposit (Fluvisols). The physical and chemical properties of the topsoil of the three sites are summarised in Table 1.

Treatments and management

The experiment consisted of maize grown following pure-species fallows of *Gliricidia sepium*, *Acaciaanguistissima*, *Leucaena collinsii*, *Leucaena diversifolia*, *Leucaena esculenta*, *Leucaena pallida*, *Calliandra calothyrsus*, *Senna siamea* and fully fertilised maize monoculture. *G. sepium* has been introduced from Latin America within the last 15 years, evaluated rigorously and it has been widely planted by farmers. *A. anguistissima* and *Leucaena* spp. have been introduced within the last 5 years, and are currently under evaluation for their suitability for soil fertility improvement in southern Africa. The treatments were arranged in a randomised complete block design with three replicates at each site. The continuously cropped monoculture maize received the recommended rate of fertiliser (200 kg ha^{-1} compound fertiliser composed of 100 g kg^{-1} N, 90 g kg^{-1} P and 80 g kg^{-1} K) applied at planting and 200 kg ha^{-1} urea applied at 4 weeks after planting. Legumes were spaced at 1×1 m, and the plot size for all treatments was 10×10 m. In November 2003, after 3 years of growth, the trees were cut back and woody material (i.e. branches >2 cm in diameter) was removed from the plots. Leaf biomass was measured by separating the total biomass into foliage (leaves + twigs), branches and stems. The leaves + twigs components were then weighed fresh and sub-samples were collected and oven-dried at 70°C for 48 h to constant weight to determine dry weight and the polyphenol content of the leaves. The litter and leafy biomass was incorporated into the soil during land preparation. Hybrid maize (MM 604) seed was then planted on the ridges made between the stumps, without fertiliser application. The spacing within and between rows was 0.30

Table 1 Physical and chemical properties of the top 20 cm of soil at the experimental sites

Soil physical/chemical property	Msekera	Kalunga	Masumba
Sand (%)	64	85	82
Clay (%)	24	8	13
Silt (%)	12	7	5
Organic carbon (mg kg^{-1})	14.0	10.0	7.0
Total inorganic nitrogen (mg kg^{-1})	6.6	2.7	6.7
Calcium (cmol$_c$ kg^{-1})	3.9	2.5	4.9
Magnesium (cmol$_c$ kg^{-1})	0.7	0.7	1.1
Potassium (cmol$_c$ kg^{-1})	0.2	0.3	0.5
Phosphorus (cmol$_c$ kg^{-1})	4.4	5.1	7.6
pH	4.7	5.1	5.9

and 0.75 m, respectively, giving a maize density of about 44,440 plants ha^{-1}. As the stumps re-sprouted (coppiced), the shoots were cut back in January, February and March, and incorporated into the soil. At the time of cutting the re-sprout biomass, samples were collected, oven-dried and weighed to determine the re-sprout biomass input. The proportion of stumps surviving per plot, hereafter called 'stump survival', was also determined at the time of sampling macrofauna.

Litter and soil sampling

To determine the nutrient content of the soil before planting the trees and maize, samples were taken from the top 0–20 cm soil in 2000. Litter was collected from fallow treatments from May to September 2003, when most species shed their leaves. Three traps were installed diagonally across a net plot of 49 m^{-2}. The litter collected from Kalunga and Msekera sites was analysed for percent organic carbon (C), polyphenol (P), nitrogen (N) and lignin (L) using standard methods (Anderson and Ingram 1993). The trees were then cut in November 2003. At cutting, leaf samples were collected from the upper part of trees, freeze-dried and analysed for leaf nitrogen and polyphenol content following the procedures for chemical analysis.

For sampling soil macrofauna, the method described by Lavelle et al. (2003) was used. Soil sampling was conducted in February–March 2005 2 to 3 months after planting the second season maize crop between the stumps. Soil samples were collected using a steel monolith sampler (25×25 and 25 cm depth) placed over a randomly selected spot and driven into the soil to ground level using a metallic mallet. Three monoliths (within 3–5 m of each other) were taken from each replicate plot, bringing the total number of sampling units per treatment to nine. The soil was removed from the sampler, macrofauna were hand-sorted and separated into higher taxa (family and order). In some taxa such as Coleoptera where both larvae and adults were found together, adults + larvae were recorded as beetles. Statistical analyses were conducted on animal counts per sampling unit (25×25 cm soil monolith).

Statistical analyses

ANOVA was done on legume biomass, and the treatment and site effects were assessed with an F test using the MIXED procedure of the SAS system (SAS 2003). The MIXED procedure was chosen because it extends the ANOVA model by providing a more flexible specification of the covariance matrix of the error, and allows for both correlation and heterogeneous variances. Preliminary test of normality (Shapiro–Wilk) and homogeneity of variance (Levene's test) of the macrofauna data indicated significant departures from normality and lack of homogeneity of variance among fixed effects. Therefore, a generalised linear modelling (GLM) approach was used.

The negative binomial distribution and mixed Poisson regression (Lawless 1987) with covariate structures were used to allow for many zero values (Fletcher et al. 2005) and for the observed dependence of variance upon mean abundance (Taylor 1961). The Poisson distribution on abundance is a natural choice for modelling counts because it arises under the assumption that animals are distributed randomly in space. However, many animal species are known to show aggregation in nature (Taylor 1961). Hence, the negative binomial model was chosen as an extension of an over-dispersed Poisson model (Royle 2004; Warton 2005). The relationship between the mean abundance (μ) and site (X_1) and legume species (X_2), was expressed as a log-linear model as follows:

$$log\,\mu = a + b_1 X_1 + b_2 X_2 \tag{1}$$

where a, b_1 and b_2 are parameters (regression coefficients) to be estimated. All model parameters were estimated via maximum likelihood using the GENMOD procedure of the SAS system. For generalised linear models, the deviance is of central importance for determining the goodness-of-fit of a model. The residual deviance (RD) divided by its corresponding degrees of freedom (DF) was used to detect over-dispersion under the Poisson model assumption. When over-dispersion (RD/DF>1) was noted under the Poisson assumption, the data were fitted to the negative binomial distribution. Type 3 likelihood ratio statistics (χ^2 and its associated probability) were used to compare sites and species. The second-order Akaike Information Criterion (AIC$_c$) correcting for small sample size (Hurvich and Tsai 1989) was used for comparing the Poisson with the negative binomial distribution model.

$$\text{AIC}_c = -2LL + 2K + \frac{2K(K+1)}{n - K - 1} \tag{2}$$

where LL is the log likelihood, K is the number of parameters in the model and n is the sample size. Smaller AIC$_c$ values indicated a more parsimonious model (Johnson and Omland 2004). Msekera site and G. sepium were held as the reference categories for comparison of sites and treatments, respectively. Abundances of the various macrofauna in soils under maize grown in legume fallows were also compared with abundance under fully fertilised monoculture maize.

To determine the quantity and quality indices that induce spatial variations in macrofauna abundance, a log-linear modelling approach (Lawless 1987) was used. Animal counts were held as dependent variables and quality and quantity indices as the explanatory variables. The (L + P) to N ratio is known to be a reliable quality index that can be

Table 2 Cumulative litter biomass (t ha−1 during the 3-year fallow period), leaf biomass (t ha^{-1} at cutting), re–sprout biomass (t ha^{-1} produced annually) and recycled biomass (t ha^{-1} added to the soil over 5 years) by the various legume species, stump survival (%) and polyphenol (PP) content of the leaf (%) at three sites in eastern Zambia

Site	Legume species	Biomass (t ha^{-1})					
		Litter	Leaf	Re-sprout	Recycled	Stump survival	Leaf PP (%)
Kalunga	A. anguistissima	4.84 a	0.83 ab	4.51 a	10.20 a	96.7 a	8.0 cd
	G. sepium	3.13 ab	2.27 a	3.96 ab	9.37 ab	97.0 a	2.0 e
	L. collinsii	3.90 ab	1.13 ab	4.55 a	9.59 ab	94.0 a	13.9 a
	C. calothyrsus	4.78 a	0.77 ab	2.84 bcd	8.39 abc	95.0 a	11.8 ab
	L.esculenta Machakos	3.30 ab	0.50 b	3.20 bc	7.00 bcd	83.3 ab	10.7 abc
	L. pallida	2.25 b	0.67 ab	3.90 ab	6.79 bcd	85.7 ab	7.3 d
	L. diversifolia 53/88	3.33 ab	0.30 b	2.00 cde	5.64 cde	64.0 b	9.2 bcd
	L. diversifolia 35/88	3.02 ab	0.37 b	1.61 de	5.02 de	62.0 b	9.3 bcd
	S. siamea	1.57 b	1.00 ab	1.38 e	3.96 e	98.7 a	8.7 bcd
	F value	4.5	3.2	23.8	15.0	7.7	38.4
	F probability	0.004	0.024	<0.001	<0.001	<0.001	<0.001
Masumba	L. collinsii	3.78	0.35 b	3.48 bc	7.58 abc	42.5 ef	9.9 a
	G. sepium	2.58	2.20 a	5.18 ab	9.95 ab	95.7 ab	2.4 d
	S. siamea	2.92	1.77 ab	3.93 abc	8.60 abc	97.0 a	6.2 b
	A. anguistissima	3.28	0.30 b	5.49 ab	9.08 abc	76.3 bc	6.1 b
	L. pallida	2.3	2.20 a	5.96 a	10.48 a	70.0 cd	3.8 cd
	L.esculenta Machakos	1.35	0.47 b	5.53 ab	7.33 abc	65.7 cde	6.1 b
	L. diversifolia 35/88	2.12	1.00 ab	1.96 cd	5.09 bc	35.3 f	6.0 b
	L. diversifolia 53/88	3.4	0.30 b	2.43 cd	6.09 abc	44.7 def	5.5 bc
	C. calothyrsus	3.57	0.13 b	1.31 d	5.03 c	29.3 f	10.0 a
	F value	2.7	7.4	18.7	4.4	25.7	30.5
	F probability	0.046	<0.001	<0.001	0.009	<0.001	<0.001
Msekera	S. siamea	3.32	2.80 a	1.30 c	7.44	85.7	6.7 bc
	L. collinsii	3.10	0.57 b	3.45 a	7.14	70.0	11.3 a
	G. sepium	2.79	0.67 b	2.57 abc	6.03	71.0	2.8 d
	A. anguistissima	2.61	0.79 b	3.70 a	6.99	80.0	6.6 bc
	L. diversifolia 53/88	2.95	0.40 b	2.26 abc	5.64	80.7	6.0 c
	L. diversifolia 35/88	2.65	0.53 b	2.27 abc	5.44	75.7	4.3 cd
	L. pallida	1.86	0.53 b	3.31 ab	5.71	76.7	5.1 cd
	L.esculenta Machakos	2.36	0.17 b	1.61 c	4.17	72.7	4.9 cd
	C. calothyrsus	2.39	0.33 b	1.75 bc	4.49	71.3	10.5 ab
	F value	1.1	3.8	6.42	2.3	0.9	14.1
	F probability	0.436	0.011	<0.001	0.075	0.512	<0.001
Combined	F value sites (DF=2)	5.3	2.3	41.8	7.9	34.4	45.1
	F probability	0.008	0.086	<0.001	<0.001	<0.001	<0.001
	F value Spp (DF=8)	4.2	6.5	31.5	8.6	14.1	58.7
	F probability	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	F sites × Spp (DF=16)	2.3	3.0	7.8	4.0	4.8	3.2
	F probability	0.014	0.002	<0.001	<0.001	<0.001	<0.001

Means followed by the same letters in a column and within site do not significantly differ at 5% level according to HSD

used as an indicator of the decomposition potential of organic inputs from agroforestry species (Mafongoya et al. 1998a,b). Based on this index, species were ranked as high, medium and low in the (L + P) to N ratio. The data on litter biomass, leaf biomass and re-sprout biomass for each species at each site were also ranked as high, medium and low. Then the relationship between the mean abundance (μ) of a macrofauna group and the explanatory variables, i.e. X_1 (litter biomass), X_2 (leaf biomass), X_3 (re-sprout biomass),

X_4 (recycled biomass), X_5 [(L + P) to N ratio] and X_6 (stump survival) was expressed as:

$$log\,\mu = a + b_1 + X_1 + b_2X_2 + \ldots + b_6X_6 \qquad (3)$$

where a, b_1 to b_6 are parameters (regression coefficients) to be estimated assuming the negative binomial distribution. The best fitting model was chosen based on the minimised second-order Akaike information criterion (AIC$_c$). For the two sites (Msekera and Kalunga) where

Table 3 Parameter estimates[a] of the negative binomial model relating abundance of the major macrofauna groups in the soil to various legume fallows and sites in eastern Zambia

Parameters	Earthworms	Ants	Termites	Beetles	Millipedes
Intercept	−0.71*	−0.63	2.26***	−0.35	−0.75
Kalunga	1.86***	−0.18	−0.20	0.46*	−0.05
Masumba	−1.27**	1.26**	−0.01	−0.75**	0.60
Msekera	0.0[‡]	0.0	0.0	0.0	0.0
A. anguistissima	−0.79*	0.002	−0.58	0.29	−0.49
C. calothyrsus	−0.91	0.53	−1.32*	0.72*	−0.66
L. collinsii	−0.23	0.97	−0.07	0.22	−0.24
L. diversifolia 35/88	−1.13*	1.58*	−0.70	−0.04	−0.53
L. diversifolia 53/88	−0.67	0.07	−0.21	−0.02	−0.47
L. esculenta Machakos	−0.69	−0.22	−0.32	0.22	−25.17**
L. pallida	−0.62	0.02	−0.18	−0.03	−0.85
S. siamea	−0.39	−0.66	−0.38	−0.28	0.31
G. sepium	0.0[b]	0.0	0.0	0.0	0.0
Site χ^2 with 2 DF	88.0***	9.7**	0.3 ns	29.1***	3.4 ns
Species χ^2 with 8 DF	8.9 ns	12.0 ns	5.7 ns	11.8*	19.0*

Negative signs before parameter estimates indicate reduction in abundance relative to the reference category, while positive signs indicate increase

ns Not significant

*Significant at 5% level

**Significant at the 1% level

***Significant at the 0.1% level

[a] Parameter estimates are regression coefficients relating abundance to sites and treatments via a logarithmic link function

[b] Msekera site and *G. sepium* were held as the reference categories for sites and species, respectively

quantitative data were available on C, P, N and L, multiple regression analysis was also conducted. The mean abundances of a macrofauna group was held as the dependent and litter biomass, leaf biomass, re-sprout biomass, C, N, P, L content of the litter, (L + P) to N ratio in the litter and stump survival as the explanatory variables.

Results

Quantity and quality of biomass

Cumulative litter biomass, leaf biomass at cutting and re-sprout biomass differed significantly with site, species and site by species interaction (Table 2). The highest (4.84 t ha^{-1}) and lowest (1.35 t ha^{-1}) litter biomass were recorded in *A. anguistissima* at Kalunga and *L. esculenta* at Masumba, respectively. Leaf biomass at cutting differed significantly according to site by species interaction (Table 2). *G. sepium* produced the highest (over 2.2 t ha^{-1}) whilst *L. diversifolia* 53/88 produced the lowest (less than 0.3 t ha^{-1}) leaf biomass at cutting at Kalunga and Masumba. At the Msekera site, *S. siamea* and *L. esculenta* produced the highest (2.8 t ha^{-1}) and lowest (0.2 t ha^{-1}) leaf biomass, respectively. Re-sprout biomass production differed significantly according to species, site and site by species interactions (Table 2). The highest (5.18 t ha^{-1}) and lowest (1.30 t ha^{-1}) re-sprout

biomass was recorded in *G. sepium* at Masumba and *S. siamea* at Msekera, respectively. *L. collinsii*, *G. sepium* and *A. anguistissima* generally produced higher recycled biomass compared to *C. calothyrsus*, *L. diversifolia* and *L. pallida* provenances. Stump survival significantly differed according to site, species and species by site interactions (Table 2).

The polyphenol (P) content of the leaf biomass differed according to site, species and species by site interactions (Table 2). At all sites the lowest and highest P contents of the leaf were recorded in *G. sepium* and *L. collinsii*, respectively. *G. sepium* produced high quality biomass with low (L + P) to N ratio. *A. anguistissima* and *L. collinsii* produced biomass with moderate (L + P) to N ratio, which is considered of medium quality. *C. calothyrsus*, *L. esculenta*, *L. pallida*, *L. diversifolia* provenances and *S. siamea* produced biomass with high (L + P) to N ratios, which is regarded as low quality. The organic C, N and L contents of the litter did not differ among the species at the two sites.

Variations in macrofaunal abundance

Macrofauna groups including earthworms, ants, termites, beetles, millipedes, centipedes and Arachnida (spiders, sun spiders, velvet mites, etc.) occurred in sufficiently large numbers to be analysed statistically. Most of the macro-

Fig. 1 Abundance (counts per 25×25 cm soil) of major macrofauna groups under maize grown in fallows of various legume species at Msekera, Kalunga and Masumba sites. *Vertical bars* indicate standard errors of means. The sample size (**n**) for each treatment at each site was 9
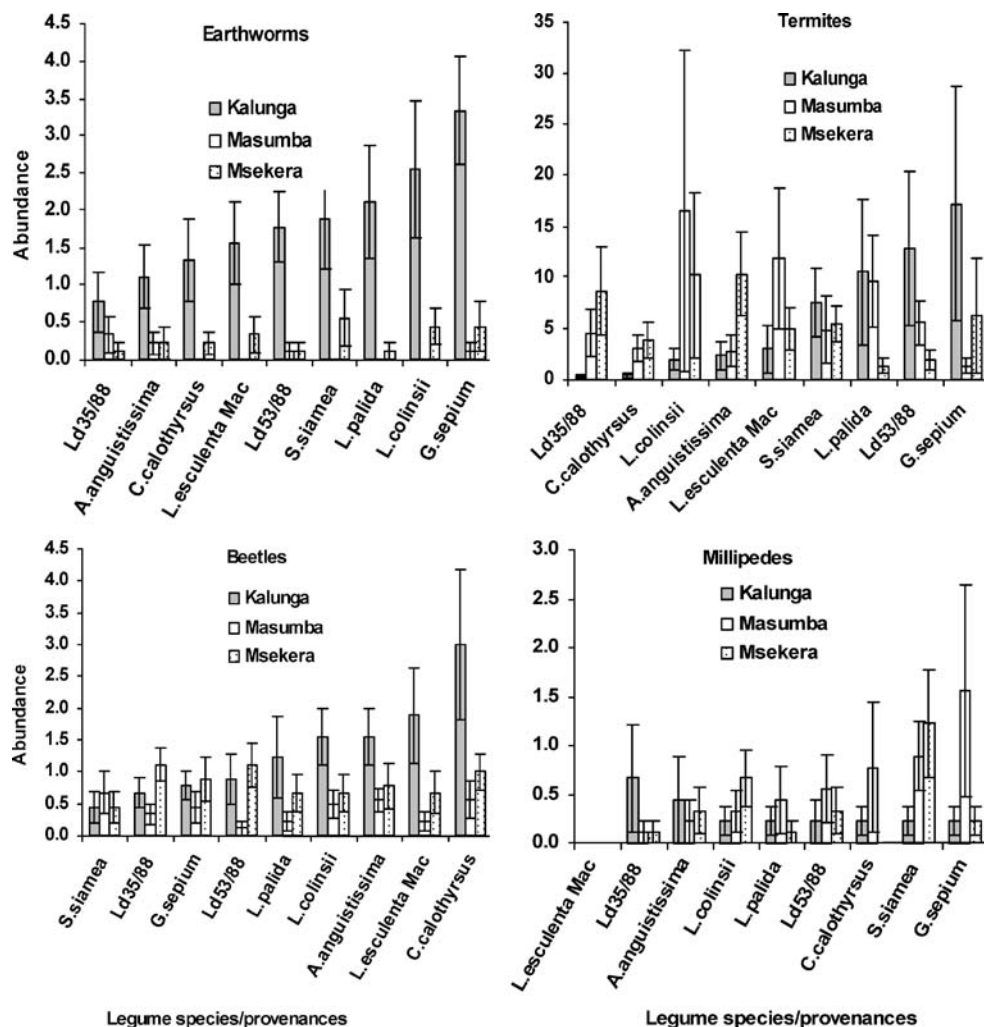
fauna groups, except centipedes and Arachnida, were over-dispersed (RD/DF>1) relative to a Poisson distribution.

Though earthworms showed under-dispersion at some sites, the negative binomial (AIC$_c$=275.1) described their overall distribution in the maize crops more parsimoniously than did the Poisson (AIC$_c$=297.7). Their abundance differed among sites and maize grown in the different fallow species (Table 3). Earthworm abundances under maize in the various legume fallows were higher at Kalunga and lower at Masumba compared with the Msekera site (Fig. 1). Earthworms were less abundant under *A. anguistissima* and *L. diversifolia* 35/88 compared with *G. sepium* (Table 3; Fig. 1). Earthworm abundance was also significantly lower under monoculture maize compared with maize grown in *G. sepium*, *L. collinsii*, *L. pallida* and *S. siamea* fallows.

At Kalunga and Msekera beetles showed over-dispersion relative to the Poisson, whilst at Masumba they were randomly distributed. However, the negative binomial (AIC$_c$=463.9) gave a better description of their overall distribution than the Poisson (AIC$_c$=477.3). Beetle abun-

dance differed significantly (Table 3) with sites and legume species (Fig. 1). Soils under maize grown in *C. calothyrsus* fallows had more beetles compared with maize grown in *G. sepium* or monoculture maize.

Millipedes were over-dispersed relative to the Poisson at Kalunga and Masumba sites, whilst they showed random distribution at Msekera. However, the negative binomial (AIC$_c$=301.7) described their overall distribution more parsimoniously than the Poisson (AIC$_c$=360.3). Though their abundance did not differ with sites, it differed with legume species (Table 3). Millipedes were absent from soils under maize grown in *L. esculenta* provenance at all sites (Fig. 1). When compared with monoculture maize, millipedes were more abundant under maize grown in *G. sepium*, *L. collinsii* and *S. siamea* fallows.

Ants and termites were over-dispersed relative to the Poisson, and their distributions were best described by the negative binomial. Ant abundance differed among sites but not among legume species. The Masumba site had more ants compared with the Msekera site (Table 3). Termites showed

Table 4 Parameter estimates[a] of the negative binomial model relating abundance of earthworms, beetles and millipedes to quantity and quality of organic inputs (data for Kalunga, Msekera and Masumba combined) in eastern Zambia

Variable	Parameters	Earthworms	Beetles	Millipedes
Intercept		−3.48***	−0.30	−2.81***
Litter biomass	High	1.22***	0.38**	NS
	Low	−0.45	−0.53*	NS
	Medium[b]	0.0	0.0	0.0
Leaf biomass	High	0.10	−0.26	NS
	Low	1.88**	0.23	NS
	Medium[b]	0.0	0.0	0.0
Re-sprout biomass	High	0.66*	−0.48***	1.09*
	Low	0.12	−0.52**	0.58
	Medium[b]	0.0	0.0	0.0
Recycled biomass	High	NS	NS	0.77*
	Low	NS	NS	−0.41
	Medium[b]	0.0	0.0	0.0
(L + P) to N	High	0.89*	NS	1.65***
	Low	1.02***	NS	−0.41
	Medium[b]	0.0	0.0	0.0
Stump survival	High	1.40***	0.48*	NS
	Low	−1.71***	−0.66*	NS
	Medium[b]	0.0	0.0	0.0

Negative signs preceding parameter estimates indicate reduction in abundance relative to the reference category, while positive signs indicate increase

NS Not significant

*Significant at 5% level

**Significant at the 1% level

***Significant at the 0.1% level

[a] Parameter estimates are regression coefficients relating abundance to sites and treatments via a logarithmic link function

[b] Medium was held as the reference category

high variability within sites and species as indicated by the large standard errors of means (Fig. 1). Though centipedes were under-dispersed at all three sites, their overall distribution fitted the negative binomial distribution (AIC_c=172.3) better than the Poisson (AIC_c=176.7).

Relation between macrofauna abundance, biomass quantity and quality

Results of the log-linear model (Eq. 3) are summarised in Table 4. The variables that influenced earthworm abundance significantly ($P<0.05$) were litter biomass, leaf biomass, (L + P) to N ratio and stump survival. Earthworms were more abundant under species that produced large quantities of litter biomass with low (L + P) to N ratio, which decomposed fast. Species with high stump survival also favoured earthworms more than those with low or moderate stump survival after cutting (Table 4). Multiple regression analysis results indicated that earthworm abundance had a significant positive association only with stump survival, which explained about 67.2% of the variation in earthworm abundance.

The log-linear model results (Table 4) showed that beetle abundance was significantly influenced by litter biomass, leaf biomass, re-sprout biomass, and stump survival.

Beetles were more abundant under species that produced high quantities of litter and moderate amount of re-sprout biomass. Legume species with high stump survival also favoured beetles more than those with low or moderate survival (Table 4). Correlation analysis showed a positive linear association of beetle abundance with litter biomass (r=0.76, $P<0.004$), N content of litter (r=0.62, P=0.033) and a negative association with C to N ratio of the litter biomass (r=0.65, $P<0.022$). Multiple regression analysis revealed a positive association of beetle abundance with litter biomass but negative association with leaf biomass, which together explained about 74.4% of the variation in beetle abundance.

Millipede abundance was significantly ($P<0.05$) influenced by re-sprout biomass, recycled biomass and (L + P) to N ratio. None of the other variables entered in the log-linear model showed significant influence on millipede abundance (Table 4). According to the multiple regression analysis, millipede abundance at the Msekera and Kalunga sites was associated positively with leaf biomass at cutting, which explained 43.0% of their variation.

The abundance of ants and termites was not influenced by any of the variables considered in the log-linear model (Eq. 3). However, multiple regression analysis showed a

positive association between termite abundance and leaf and re-sprout biomass, but negative association with litter biomass and polyphenol content of the litter at the Msekera and Kalunga sites. Together, these factors accounted for 84.2% of the explained variation in termite abundance in soils under the agroforestry species.

Discussion

The results show that the quantity and quality of biomass produced by the legume species had impact on the abundance of macrofauna except on centipedes and Arachnida, which had a random spatial distribution. The residual deviance and AIC_c values indicated over-dispersion in the distribution of earthworms, beetles, millipedes, ants and termites, which was adequately described by the negative binomial model. The existence of over-dispersion relative to the Poisson may be interpreted as an indication of habitat heterogeneity or biological phenomenon such as aggregation (Fletcher et al. 2005). The spatial heterogeneity in organic resource quality and quantity apparently explained most of the observed variation in the abundance of earthworms, beetles and millipedes. Beetles and millipedes, which are litter transformers, were influenced probably because they feed directly on the biomass incorporated in the soil. Stump survival influences earthworms and beetles probably by ameliorating the surface soil temperature and moisture by the continuous re-sprouting of stumps.

Though not clear at all sites, variations in termite abundance were partially explained by organic matter quantity and quality at least at the Kalunga and Msekera sites. The lack of significant association between their abundance and (L + P) to N ratios is probably because these invertebrates are able to use a variety of organic resources available in the soil systems. Termites are known to have sophisticated digestive systems with symbiotic microflora allowing them to feed on wood, leaf litter, dead or live roots and different fractions of soil organic matter. Lack of a complex digestive system in millipedes may account for the significant effect of lignin content of organic inputs on millipedes. Ants, centipedes and Arachnida, which are predators, were not affected either by the quantity or quality of biomass. The spatial aggregation observed in ant distributions may not be related to organic inputs, but to other biological phenomena such as their nesting and foraging habits.

The results emphasise the importance of both quantity and quality of organic inputs in the maintenance of diverse soil macrofauna. Active communities of macrofauna in the soil could be maintained by practices that provide plant cover and diverse organic inputs. The coppicing fallow practice may thus provide an opportunity to do that. Diversity of organic inputs may be increased especially by mixed planting (Mafongoya et al. 2006) of leguminous fallow species. Further research is needed on the effect of these practices on other fauna such as nematodes and mesofauna to formulate recommendations.

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