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Original article The influence of litter quality and micro-habitat on litter decomposition and soil properties in a silvopasture system

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ABSTRACT

Studies to understand litter processes and soil properties are useful for maintaining pastureland productivity as animal husbandry is the dominant occupation in the hot arid region. We aimed to quantify how micro-habitats and combinations of litters of the introduced leguminous tree Colophospermum mopane with the grasses Cenchrus ciliaris or Lasiurus sindicus influence decomposition rate and soil nutrient changes in a hot desert silvopasture system. Litter bags with tree litter alone (T), tree + C. ciliaris in 1:1 ratio (TCC) and tree + L. sindicus 1:1 ratio (TLS) litter were placed inside and outside of the C. mopane canopy and at the surface, 3-7 cm and 8-12 cm soil depths. We examined litter loss, soil fauna abundance, organic carbon (SOC), total (TN), ammonium (NH₄-N) and nitrate (NO₃-N) nitrogen, phosphorus (PO₄-P), soil respiration (SR) and dehydrogenase activity (DHA) in soil adjacent to each litter bag. After 12 months exposure, the mean residual litter was 40.2% of the initial value and annual decomposition rate constant (k) was 0.98 (0.49–1.80). Highest (p < 0.01) litter loss was in the first four months, when faunal abundance, SR, DHA and humidity were highest but it decreased with time. These variables and k were highest under the tree canopies. The litter loss and k were highest (p < 0.01) in TLS under the tree canopy, but the reverse trend was found for litter outside the canopy. Faunal abundance, litter loss, k, nutrient release and biochemical activities were highest (p < 0.01) in the 3–7 cm soil layer. Positive correlations of litter loss and soil fauna abundance with soil nutrients, SR and DHA demonstrated the interactions of litter quality and micro-habitats together with soil fauna on increased soil fertility. These results suggest that a Colophospermum mopane and L. sindicus silvopasture system best promotes faunal abundance, litter decomposition and soil fertility. The properties of these species and the associated faunal resources may be utilised as an ecosystem-restoration strategy in designing a silvopasture system. This may help to control land degradation and increase productivity sustainably in this environment.

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1. Introduction

Adequate supply of fodder and food to meet the needs of everincreasing populations of humans and livestock is a major challenge for most developing countries, especially in dry areas. Indian arid zone is characterized by psammophytic desert vegetation to xeromorphic thorn forest (Champion and Seth, 1968). Immense disturbance, caused by cultivation and grazing leads to a rare climax system, and presently what we see is a totally transformed ecosystem (Dhir, 2003). The damaging effects of the current land use and management are on grazing lands, i.e. pasturelands and the cultivated wastelands on which the economy of the most of the people of this region depends (Khurana, 1997). The focus on production systems should therefore, be widened to include the problem of how best to conserve and utilize these natural resources and biodiversity while achieving optimum sustainable yields. As the process of nutrient turnover and litter decomposition is critical for maintaining the functioning of natural and managed ecosystems, particularly in dry areas, a better understanding of litter decomposition and involvement of soil fauna is a step towards improving productivity of land use systems (Knoepp et al., 2000; Wu et al., 2009).

Soil fauna and microbes affect soil function in a variety of ways and are used as indicators of nutrient status of soil (Rao et al., 1998; Vanlauwe et al., 1997). Growth of soil microbes as a result of inputs of high carbon and low nitrogen substrates results in the immobilization of soil nitrogen in the rapidly growing microbial biomass (Jiménez et al., 2009). Many studies have demonstrated the importance of soil fauna in nutrient cycling (Anderson et al., 1985;





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Oyedele et al., 2006), biological indices (Knoepp et al., 2000) and breakdown of leaf litter/crop residues (Lal, 1999; Gonzalez and Seastedt, 2001; Miranda et al., 2009). Thus belowground faunal resources help improve soil fertility by their facilitative effects on litter reduction, decomposition and nutrient release to enhance rangeland productivity (Schädler and Brandl, 2005a). However, attributes of litter decomposition are determined by litter traits and climatic conditions (Adair et al., 2008; Cornwell et al., 2008; Frouz, 2008). But the results on litter-species interactions are variable, ranging from clearly negative to strongly positive litter mixing effects on decomposition (Wardle et al., 1997; Gartner and Cardon, 2004; Hättenschwiler, 2005). This presents a need to study the role of soil fauna in decomposition of mixed litter of tree and grasses for better understanding of nutrient turnover and improvement in soil conditions of desert silvopasture.

Colophospermum mopane (Kirk ex Benth.) Kirk ex J. Léonard, a leguminous tree introduced to India from low altitude, high temperature regions of southern Africa (Coates, 1983), is a multipurpose species of degraded lands (Singh, 2003, 2005; Singh and Rathod, 2007). C. mopane is now planted with climax perennial grass species like Lasiurus sindicus Henrard and Cenchrus ciliaris L. under silvopasture. In the present scenario of desertification, there is a need to control soil degradation and improve productivity of hot desert pasturelands by integrating trees and using the soil faunal community as an eco-engineer to improve decomposition of litter and nutrient release in a mixed litter of trees and grasses. Therefore, the objectives of this study were to quantify (i) the effects of microhabitats and combinations of litters of the tree C. mopane and the grasses C. ciliaris and L. sindicus on soil faunal abundance: and (ii) the influence of the faunal abundance on litter decomposition and consequent changes in soil nutritional and biochemical properties, in silvopasture systems. We used mixed litters of C. mopane, C. ciliaris and L. sindicus to test how combinations of litters of these species influence litter decomposition rate (Hobbie, 2005), which may be further influenced by total faunal abundance associated with the litter, tree shading and litter position in the soil.

2. Materials and methods

2.1. Site conditions

Studies were conducted in Jodhpur district, situated between 26°45′N latitude and 72°03′E longitude in the arid region of India.

The climate of the region is dry tropical type. The maximum temperature was 41.5 °C in summer and the minimum temperature was 10 °C in winter during 2004–2005 (CAZRI, 2005). Monthly rainfall varied from 0.2 to 140 mm with average number of rainfall days of 15–21 per annum. Average wind speed was 14–18 km h⁻¹, which reached as high as 60–70 km h⁻¹ in summer. Potential evapotranspiration was exceedingly higher than the precipitation resulting in perpetual water deficit throughout the year (Rao and Miyazaki, 1997). The experimental farm was flat land with loamy sand soil (coarse loamy, mixed hyperthermic family of typic camborthids according to US soil taxonomy) underlained with a thick concretion of calcium carbonate at a depth of 75 cm (Sehgal, 1990).

2.2. Experimental procedures

Six trees of *Colophospermum mopane* having an average height of 3.9 m, crown diameter of 3.8 m and collar girth of 22.8 cm (15 cm above from soil surface) were selected randomly from a population covering 4 ha area and raised under a silvopasture system. The grasses grown in association with C. mopane trees were C. ciliaris and L. sindicus, two important fodder grasses of the Indian desert. Dry fallen litter of Colophospermum mopane and the grasses C. ciliaris and L. sindicus were collected in June 2004 (a time of maximum accumulated litter), chopped and allowed to dry. Leaves of C. mopane contain 14.1% crude protein, 0.99% Ca, 0.205% Mg, 0.786% K, 0.0049% Na, 0.156% P, 55.9 mg kg⁻¹ Mn, 8.1 mg kg⁻¹ Cu and 3.1 mg kg⁻¹ Co on dry matter basis (Lukhele and van Ryssen, 2000). Cenchrus ciliaris and Lasiurus sindicus contain 4.73% and 4.98% crude protein (Gupta and Joshi, 1984), 1.28% and 0.58% Ca, 0.27% and 0.16% Mg, 2.70% and 0.10% Na, 3.30% and 2.80% K, 0.31% and 0.20% P, 81.7 mg kg⁻¹ and 81.7% Mn, 35.0 mg kg⁻¹ and 32.7 mg kg⁻¹ Cu, and 28.2 mg kg⁻¹ and 20.4 mg kg⁻¹ Zn, respectively (Joshi and Gupta, 1984).

One hundred grams of (i) *C. mopane* tree litter alone (T), (ii) *C. mopane* tree + *C. ciliaris* grass litters in 1:1 ratio (TCC) and (iii) *C. mopane* tree and *L. sindicus* grass litters in 1:1 ratio (TLS) were kept in a nylon bag of 7 mm mesh size for easy movement of soil fauna and protecting the litters. The litter bags were placed either a) 1 m away from the tree trunk (inside the tree canopy), or b) 2 m away from canopy zone (outside the canopy zone of trees). In each zone, the litter bags were placed in triplicate at the soil surface, and at 3-7 cm and 8-12 cm soil depths in July 2004, before the onset of the monsoon. Litter bags were pinned to protect them from wind

Table 1

Repeated measure ANOVA of litter loss, faunal abundance, soil parameters and soil biochemical properties in a Colophospermum mopane tree-based silvopasture system in the Indian desert.

Variables	Litter loss (%)	Fauna	SOC	Total N	NH₄−N	NO ₃ -N	PO ₄ -P	SR	DHA
		(#/100 g litter)	$(mg kg^{-1})$	$(mg kg^{-1})$	$(mg kg^{-1})$	$(mg kg^{-1})$	$(mg kg^{-1})$	$(mg CO_2/m^2/h)$	(p kat/g)
- 1 - 6 6									(1 10)
F values of test of v	within-subject effe	cts							
Month (M)	217.28*	441.77*	12.40*	43.47*	2.71	4.58*	41.79*	1005.40*	269.23*
$M \times Layer(D)$	0.79	11.79*	0.14	1.10	1.05	0.24	2.90*	6.59*	0.64
$M \times Canopy(C)$	1.80	19.88*	0.02	2.29	0.18	1.69	1.17	23.54*	16.0.92*
$M \times Litter (L)$	0.25	2.97*	0.27	0.48	0.17	4.10*	1.27	0.29	5.69*
$M \times D \times C$	0.33	2.43*	0.02	0.05	0.07	1.55	1.21	1.68	0.65
$M \times D \times L$	0.34	6.62*	0.03	0.25	0.12	0.38	1.01	0.79	0.26
$M \times C \times L$	0.24	0.18	0.11	0.39	0.14	0.44	1.53	3.44*	1.75
$M \times D \times C \times L$	0.09	0.47	0.14	0.07	0.07	0.69	1.07	0.42	0.34
F values of test of between-subject effects									
D	308.97*	116.03*	26.08*	15.28*	21.95*	51.69*	32.64*	24.22*	26.33*
С	137.29*	195.21*	22.2*	33.23*	37.92*	104.63*	69.55*	121.23*	103.88*
L	36.57*	5.69*	4.68*	0.99	1.88	4.35*	2.21	1.84	0.75
$D \times C$	2.87	11.36*	0.83	0.83	0.01	0.74	4.12*	3.65*	1.44
$D \times L$	15.04*	53.27*	1.06	0.90	0.50	0.54	1.68	0.27	0.42
$C \times L$	5.83*	2.22	3.06*	0.88	0.64	4.63*	0.60	0.62	0.11
$D \times C \times L$	1.28	3.50*	0.43	0.54	0.09	1.24	0.97	0.04	0.08

M, month of soil sampling, D, soil layer. Significant at *, p < 0.05, **, p < 0.01.

blowing. Thus there were 324 litter bags (3 litter qualities \times 2 canopy zones \times 3 places + 3 depths \times 6 replications). Litter bags from each location were collected at the 4th month (i.e., October 2004), 8th month (i.e., February 2005) and 12th months (i.e., June 2005) after placement. The initial 4 months coincided with the monsoon, 5th to 8th months with winter and last 9–12 months coincided with the summer. The decomposition rate constant (*k*), was calculated from the simple exponential decay equation:

$$\ln\left(M_0/\mathrm{Mt}\right) = k^* i$$

where M_0 = mass of litter at time 0, Mt = mass of litter at time t, t = time duration of litter decomposition, and k = decomposition rate constant. Half lives ($t_{0.5}$) of decomposing litter samples are estimated from the values as follows: $t_{0.5} = 0.693/k$. Similarly, time taken for 95% decomposition was estimated as: $t_{0.95} = 2.9957/k$ (Chapin III et al., 2002).

The fauna associated with litter (litter bags) was extracted by hand-sorting and using a Tullgren funnel. In the Tullgren funnel, 60

Watt bulbs were regulated by a rheostat control. Animals were allowed to move downwards in the funnel for 24 h and they were stored in 70% alcohol. After extraction, the different groups of arthropods were sorted out using a stereoscopic microscope and the specimens were picked up with the help of a bristle, and preserved for further grouping and identification in separate vials. Fauna were grouped on the basis of their major categories such as mites, Collembola, pseudoscorpions, beetles etc. (Tripathi et al., 2005). Smaller soil fauna were processed for slide preparation. They were dehydrated in graded alcohol series, stained in eosin, and mounted in DPX for observations.

Soil samples were collected from each place where a litter bag was removed (mentioned above). A single core was excavated to a depth of 0-15 cm and divided into top 0-2 cm, 3-7 cm and 8-12 cm soil layers. Soil samples were air-dried and passed through a 2 mm mesh-sieve. Soil organic carbon (SOC), total nitrogen (TN), ammonium nitrogen (NH₄–N), nitrate nitrogen (NO₃–N) and available phosphorus (PO₄–P) were estimated as described by Anderson and Ingram (1993) and Walkley and Black (1934). Soil



Fig. 1. Changes in faunal abundance (left panels) and loss of litter (right panels) of varying quality in a *Colophospermum mopane* tree-based silvopasture system. T: *C. mopane* litter only; TCC: *C. mopane* + *Cenchrus ciliaris* litter in 1:1 ratio; TLS: *C. mopane* + *Lasiurus sindicus* litter in 1:1 ratio. (–) outside tree canopy; (+) inside tree canopy. Error bars are ±SE of six replicates.

respiration (SR) and soil dehydrogenase activity (DHA) – an indicator of the oxidative metabolism in soils and thus of the microbiological activity (Skujins, 1973), were determined using potassium hydroxide (KOH) and triphenyl tetrazolium chloride (TTC), respectively (Singh et al., 1999).

2.3. Statistical analysis

Data on litter loss (decomposition), soil organic carbon, nutrient dynamics and biochemical changes were analysed using the SPSS statistical package (Levesque, 2007). Since the observations were recorded repeatedly from the same site i.e. 4 months, 8 months and 12 months after placing the litter bags, the data were subjected to repeated measures ANOVA to test the level of significance. Months were tests of within subject effects, whereas litter quality, soil layer and canopy zone were tests of between subject effects. Duncan's Multiple Range Test (DMRT) was performed to obtain homogeneous subsets among the litter qualities and soil layers. Pearson correlation coefficients were calculated to examine the relationships between the soil fauna population with litter decomposition and soil chemical and biochemical properties. The level of significance was set at 0.05.

3. Results

3.1. Environmental variables

Air temperature was highest during April (41.5 °C and 28.9 °C for mean monthly maximum and minimum temperatures, respectively), with a slight decline in July–August, the air temperature increased again in October before dropping down to their lowest levels in January (23.4 °C and 10.0 °C for mean monthly maximum and minimum temperatures, respectively). Most of the rainfall was received during July to September (236 mm and 186 mm in 2004 and 2005, respectively), which increased relative humidity to the highest value (86% and 54% for monthly maximum and minimum relative humidity, respectively) in August. After decreasing in October the relative humidity increased again in December– January (i.e., winter season), but before reaching the highest in August, it again decreased to the lowest value in March/April (31% and 11% for monthly maximum and minimum relative humidity, respectively).

3.2. Faunal abundance dynamics

Differences in abundance of soil fauna associated with litter were significant (p < 0.01) between seasons, i.e. sampling times (Table 1). Faunal abundance was highest (100 fauna 100 g^{-1} litter) at the 4th month of sampling i.e., July to October 2004 and lowest after 12 months (43 fauna 100 g⁻¹ litter) and 8 months (51 fauna 100 g⁻¹ litter). All the interaction terms viz. seasons \times depth, seasons \times canopy, seasons \times litter quality, seasons \times depth \times canopy, seasons \times depth \times litter quality were significant (p < 0.05). Tests of between-subjects effects indicated variation (p < 0.01) in animal abundance due to tree canopy zone, litter quality and soil layer of litter bag placement. Irrespective of litter quality and soil layer, faunal abundance was 120 individuals 100 g^{-1} at 4 months, 60 individuals 100 g^{-1} at 8 months and 50 individuals 100 g^{-1} litter at 12 months under the canopy zone (p < 0.01) as compared to 81 individuals 100 g⁻¹, 41 individuals 100 g⁻¹ and 35 individuals 100 g⁻¹ litter, respectively outside the canopy zone of the C. mopane tree (Fig. 1 left panels). Among litter quality treatments, faunal abundance was highest (p < 0.01) for TLS litter inside the canopy and lowest for TCC litter outside the tree canopy throughout the year. Among soil layers, faunal abundance was highest in the 3-7 cm soil layer, whereas it was

lowest in the litter bags placed in the 8–12 cm soil layer. Significant (p < 0.05) layer × canopy × litter quality interaction indicated highest animal abundance in TLS at 4th and 8th months of sampling in the 3–7 cm soil layer under the tree canopy and the lowest abundance was for TLS in the surface litter bags outside tree canopy throughout the study period.

3.3. Litter loss/decomposition rate

Differences in the litter loss were significant (p < 0.01) due to months (when litter loss was measured). Average litter loss was about 40.1% during the first four months, 10.8% at 5-8 months, and 8.6% in the 9th–12th months with cumulative litter loss of 51.2% after 8 months and 59.8% after 12 months (Table 1). The test of between subject effects showed that litter loss varied (p < 0.01) between canopy zone, litter quality and soil layers of litter bag placement (Fig. 1 right panels). Irrespective of soil layer and litter quality, litter loss was 18.0% greater (p < 0.01) under the canopy than outside the canopy zone of the C. mopane trees. Considering litter quality, litter loss was highest (p < 0.01) in TLS (63.4%) and lowest in TCC (57.7%). Litter loss was highest (p < 0.01) in the 3– 7 cm soil layer (72.0%) and lowest in surface placed litter bags (48.5%). All interaction terms were significant (p < 0.05). Significant (p < 0.01) canopy × litter quality × soil layer interaction showed highest litter loss in TLS litter below the canopy, and lowest loss in T litter alone outside tree canopy throughout the year.

Litter decomposition was faster (p < 0.01) under the tree canopy than outside of the tree canopy (k ranged from 0.494 to 1.794, Table 2). Across tree canopy and soil layer positions, decomposition was fastest (p < 0.01) for TLS litter. The variation in decomposition rate between the tree litter alone and TCC litter was not significant (indicated by DMRT). Decomposition was fastest for the litter placed in the 3–7 cm soil layer and slowest for the litter placed at the soil surface. The interaction terms were not significant except for litter quality × soil layer showing dependency of litter decomposition on litter quality and the position of the litter in soils. The half life and the time taken for 95% of litter decomposition was 0.40 year and 1.73 year, respectively for TLS placed in the 3–7 cm soil

Table 2

Litter decomposition constants (*k*), half life ($t_{0.5}$) and time taken for 95% decomposition of litters of varying combinations (i.e. quality) in a *Colophospermum mopane* tree-based silvopasture system. Values are mean \pm SE of six replicates.

Soil layer	Canopy Litter zone quality		Decomposition rate constant (k)	Time taken in litter decomposition (year)		
			12 Month (June)	50% (<i>t</i> _{0.05})	$0.95\%(t_{0.95})$	
Surface	Outside	T-	$\textbf{0.494} \pm \textbf{0.037}$	1.445 ± 0.109	6.244 ± 0.472	
		TCC-	0.536 ± 0.041	1.332 ± 0.104	5.759 ± 0.454	
		TLS-	0.619 ± 0.054	1.165 ± 0.105	5.036 ± 0.454	
	Inside	T+	0.722 ± 0.038	0.973 ± 0.049	4.206 ± 0.215	
		TCC+	0.945 ± 0.079	0.761 ± 0.065	$\textbf{3.289} \pm \textbf{0.280}$	
		TLS+	0.777 ± 0.047	0.910 ± 0.060	3.935 ± 0.259	
$5\pm 2\ cm$	Outside	T-	1.093 ± 0.122	0.675 ± 0.074	$\textbf{2.916} \pm \textbf{0.319}$	
		TCC-	0.958 ± 0.063	0.739 ± 0.049	$\textbf{3.196} \pm \textbf{0.211}$	
		TLS-	1.436 ± 0.109	0.497 ± 0.038	2.148 ± 0.163	
	Inside	T+	1.505 ± 0.168	0.490 ± 0.053	$\textbf{2.119} \pm \textbf{0.232}$	
		TCC+	1.275 ± 0.108	0.563 ± 0.046	2.435 ± 0.203	
		TLS+	1.794 ± 0.146	0.399 ± 0.032	1.725 ± 0.138	
$10\pm2~cm$	Outside	T-	0.824 ± 0.076	0.879 ± 0.083	$\textbf{3.799} \pm \textbf{0.359}$	
		TCC-	0.719 ± 0.067	1.006 ± 0.092	4.347 ± 0.394	
		TLS-	0.937 ± 0.092	0.777 ± 0.077	$\textbf{3.357} \pm \textbf{0.332}$	
	Inside	T+	0.995 ± 0.076	0.717 ± 0.055	3.101 ± 0.239	
		TCC+	0.957 ± 0.059	0.738 ± 0.046	$\textbf{3.192} \pm \textbf{0.198}$	
		TLS+	1.056 ± 0.129	0.709 ± 0.087	3.065 ± 0.376	

T, tree litter alone, TCC, tree + *Cenchrus ciliaris* (1:1 ratio) litter, TLS, tree + *Lasiurus sindicus* (1: 1 ratio) litter.

-, outside tree canopy, +, inside tree canopy.

layer under the tree canopy as compared to the highest time (1.45 year and 6.24 year, respectively) taken for T litter alone placed at the soil surface and outside the tree canopy (Table 2).

3.4. Soil organic carbon and nutrients

Soil had an average soil organic matter content (0–10 cm soil layer) of 0.27%, total nitrogen of 0.04%, available PO₄–P of 7.54 mg kg⁻¹, NO₃–N of 2.43 mg kg⁻¹ and NH₄–N of 5.14 mg kg⁻¹ soil in June 2004. Average soil organic carbon (SOC) differed (p < 0.001) between the sampling times (Fig. 2 left panels). The SOC increased with time and was highest at the 12th month of sampling. The increase in SOC was about 1.5-fold, 1.6-fold and 1.7-fold at 4, 8 and 12 months of soil sampling, respectively as compared to the initial value in June 2004. Considering the mean of all variables for the tree canopy zone, SOC was highest (p < 0.001) inside the canopy than outside the canopy zone throughout the year. Among litter quality treatments, SOC was highest (p < 0.001) in TCC and

lowest in T litter alone. SOC was highest (p < 001) in the top soil layer, i.e. soil of the surface placed litter bags and lowest at the 3–7 cm soil layer. The increase in SOC was 1.7-fold in the surface layer and 1.6-fold in the 8–12 cm soil layer at the 12th month of sampling than the initial values in the respective soil layers.

Total nitrogen increased from 0.05% at the 4th month to 0.15% at the 8th month and 0.12% at the 12th month of sampling, but the availability of NH₄–N increased to the highest (p < 0.01) value after 12 months (2.5-fold) after a slight decrease towards the 8th month (2.3-fold). NO₃–N was highest at the 4th month and it decreased towards the 12th month, though these soil variables were greater than the initial values in June 2004. The increases in total nitrogen (Fig. 2 right panels) and NH₄–N (Fig. 3 left panels) were 1.4- to 3.0-fold and 2.3- to 2.5-fold, respectively, whereas that of NO₃–N (Fig. 3 right panels) was 1.8- to 2.0-fold as compared to the initial values. Tests of between subject effects indicated significant (p < 0.01) variation in TN, NH₄–N and NO₃–N concentrations between the canopy zones, litter qualities and soil layers. Irrespective of litter



Time interval (month)

Fig. 2. Changes in soil organic carbon and total nitrogen in the soil adjacent to litter bags placed at different soil depths in a *C. mopane* tree-based silvopasture system. T: *C. mopane* litter only; TCC: *C. mopane* + *Cenchrus ciliaris* litter in 1:1 ratio; TLS: *C. mopane* + *Lasiurus sindicus* litter in 1:1 ratio. (–) outside tree canopy; (– –) inside tree canopy. Error bars are ±SE of six replicates.

quality and soil layer for canopy zone, concentrations of TN (1.3fold), NH₄-N (1.3-fold) and NO₃-N (1.3-fold) were highest (p < 0.001) under the canopy zone than outside the canopy zone of the trees (Figs. 2 and 3). The increase in these soil variables were almost 1.8- to 2.4-fold greater than their initial values in June 2004. Among litter quality, the total nitrogen and NH₄-N concentrations did not vary (p > 0.05). However, NO₃–N varied significantly (p < 0.001). Average values of TN. NH₄-N and NO₃-N were highest in TCC/TLS litters (Fig. 3). While considering the soil layers, TN, NH₄–N and NO₃–N concentrations were highest (p < 0.001) in the 3-7 cm soil layer and lowest in the surface soil. All the interaction terms were significant (p < 0.05) for these soil variables. Tree canopy \times litter quality \times soil layer interaction term (p < 0.05) showed highest TN in TLS+ and NH₄-N in TLC+ in the 3-7 cm soil layer, whereas their lowest values were in T litter alone placed in the surface soil layer outside the tree canopy.

Soil available phosphorus (PO₄-P) varied significantly (p < 0.001) between the sampling times (Table 1). Availability of PO₄-P increased with time being highest at the 12th month of sampling (Fig. 4). The average increase in PO₄-P availability was about 2.2-fold after 4 months, 2.7-fold after 8 months and 2.9-fold after 12 months of litter decomposition as compared to the initial values. All the interaction terms of repeated measure ANOVA were significant (p < 0.05). Tests of between subject effects indicated the highest (p < 0.05) concentration of PO₄–P under the canopy than outside the canopy of the trees, though the increase in PO₄-P was 3.2-fold outside the canopy and 2.5-fold under the canopy than the initial values. Availability of PO₄–P did not vary (p > 0.05) due to litter quality, though it was highest in TLS and lowest in T litters. In the case of soil layers, PO₄–P was highest in the 3–7 cm soil layer (Fig. 4) and lowest in the surface soil. Canopy \times litter quality \times soil layer interaction was significant (p < 0.05).



Time interval (month)

Fig. 3. Changes in soil available ammonium nitrogen (NH₄–N) and nitrate nitrogen (NO₃–N) in the soil adjacent to litter bags placed at different soil depths in a *C. mopane* treebased silvopasture system. T: *C. mopane* litter only; TCC: *C. mopane* + *Cenchrus ciliaris* litter in 1:1 ratio; TLS: *C. mopane* + *Lasiurus sindicus* litter in 1:1 ratio. (–) outside tree canopy; (– – –) inside tree canopy. Error bars are ±SE of six replicates.



Fig. 4. Changes in soil available phosphorus (PO₄-P) in the soil adjacent to litter bags placed at different soil depths in a *C. mopane* tree-based silvopasture system. T: *C. mopane* litter only; TCC: *C. mopane* + *Cenchrus ciliaris* litter in 1:1 ratio; TLS: *C. mopane* + *Lasiurus sindicus* litter in 1:1 ratio. (-) outside tree canopy; (- - -) inside tree canopy. Error bars are \pm SE of six replicates.

3.5. Soil biochemical changes

Soil respiration (SR) and dehydrogenase activity (DHA) differed significantly (p < 0.001) between the sampling times (Table 1). Season \times canopy, soil layer \times canopy and month \times canopy \times litter quality interactions were significant (p < 0.05) for both these variables. These variables were highest (p < 0.01) in the 4th month of observations, i.e. 5.2-fold and 3.3-fold for SR and DHA, respectively. After the 8th and 12th months of litter decomposition, SR was 1.8fold and 1.5-fold greater, whereas DHA was 2.1-fold and 1.8-fold greater than the initial values in June 2004 (Fig. 5). The tests of between subject effects showed highest (p < 0.01) values for SR and DHA in soil under the canopy than outside the tree canopy. Soil respiration and DHA did not vary (p > 0.05) within litter quality, though SR was highest in the T litter alone but DHA was highest in TLS litter. Irrespective of canopy zone and litter quality, SR and DHA were highest (p < 0.01) in the 2–5 cm soil layer, whereas their values were lowest (p < 0.01) in the surface layer throughout the study period. Significant (p < 0.01) canopy \times litter quality \times soil layer interactions indicated highest SR and DHA in TLS after 4 months and in the tree litter under the canopy after 8 months and 12 months of litter decomposition in the 3–5 cm soil layer.

3.6. Correlations between litter decomposition, soil fauna and soil variables

Litter loss showed significant (p < 0.01) positive correlations with soil nutrients (NH_4 –N, NO_3 –N and PO_4 –P) and biochemical properties (SR and DHA), but it was negatively correlated to soil organic carbon (Table 3). Faunal abundance associated with decomposing litters showed positive correlations with litter loss (r = 0.423 to 0.661, P < 0.001), total nitrogen (r = 0.317 to 0.194)p < 0.05), NH₄-N (r = 0.407 to 0.252, p < 0.001) and NO₃-N (r = 371 to 0.411, p < 0.001) at all the sampling times, i.e. 4th, 8th and 12th months of sampling (Table 3). We did not find a correlation between faunal abundance and SOC, whereas decomposition rate constant was positively (p < 0.01) correlated both to litter loss and faunal abundance. Soil available PO₄-P was also positively related with litter-associated faunal abundance in all the months of recording. Both SR and DHA also showed a positive correlation (p < 0.001) with faunal abundance associated with litter decomposition in different seasons.

4. Discussion

4.1. Factors affecting litter decomposition

Highest litter loss during the initial four months was related to rainfall period, quantity of litter availability and favourable microhabitats influencing litter decomposition (Lindsay and Cunningham, 2009). Brinson (1977) and Vander Drift (1983) highlighted the importance of rainfall and temperature in litter decomposition because these variables affect both the development of plant cover and the activities of soil fauna. The relatively greater loss and decomposition rate of TLS litter under the canopy than other litters reflected the effects of litter quality and chemistry (Gupta and Joshi, 1984; Joshi and Gupta, 1984; Zhou et al., 2008; Ramírez et al., 2009). L. sindicus is a naturally recruited best fodder grass species in the Indian desert, where time for decomposing 50% (k_{0.5}) and 95% (k_{0.95}) of litter were 0.40 year and 1.73 year, respectively. The litter decomposition rate in the present study was relatively greater compared to the data for broadleaved-Korean pine forests (Chen et al., 2010), but was less than the k values (1.24-1.80) for Acacia mangium litter (Castellanos-Barliza and Pelàez, 2011). Tree shading improved soil water due to reduced soil water loss under the tree canopy, which increased the values of litter loss and k compared to outside the canopy, though it was also influenced by the faunal abundance (Faminow and Rodriguez, 2001). This showed the importance of microhabitats facilitating litter decomposition together with faunal growth, similar to the observation of Yoshida and Hijii (2011). Better microhabitat in the 3–7 cm soil layer under the tree canopy, together with faunal abundance, facilitated litter decomposition resulting in the highest k value. However, k was also influenced heavily by soil fauna. The modified microhabitat probably enhanced the growth and development of soil fauna and facilitated litter decomposition and nutrient release similar to the observation of Wang et al. (2010).

4.2. Faunal abundance

Increase in soil moisture through rainfall, substrate (litter) availability and greater relative humidity during the monsoon period favoured an increase in soil faunal abundance (Miranda et al., 2009). Thus, sufficient availability of litter as food and relatively better microhabitat (through shade and humidity)



Fig. 5. Changes in soil respiration and dehydrogenase activity in the soil adjacent to litter bags placed at different soil depths in a *C. mopane* tree-based silvopasture system. T: *C. mopane* litter only; TCC: *C. mopane* + *Cenchrus ciliaris* litter in 1:1 ratio; TLS: *C. mopane* + *Lasiurus sindicus* litter in 1:1 ratio. (–) outside tree canopy; (- - -) inside tree canopy. Error bars are ±SE of six replicates.

Table 3

Correlation coefficients (*r*) and significance levels for the relationships between faunal abundance with litter loss, SOC, soil nutrients, soil respiration (SR) and dehydrogenase activity (DHA) in *C. mopane* tree based silvopasture system recorded at different sampling times in Indian desert.

Variables	Litter loss (%) at different month			Faunal abundance in litter bag (number of individuals per 100 g)			
	4 Months	8 Months	12 Months	4 Months	8 Months	12 Months	
Faunal population	0.723***	0.693***	0.661***	_		_	
Litter loss	-	_	_	0.723***	0.693***	0.661***	
SOC	-0.330**	-0.176NS	-0.225^{*}	0.091NS	0.022NS	0.06NS	
Total N	0.381***	0.472***	0.451**	0.249**	0.317**	0.194*	
NH ₄ -N	0.337***	0.378**	0.391**	0.252**	0.407***	0.327**	
NO ₃ -N	0.372***	0.419***	0.503***	0.411**	0.381**	0.371**	
PO ₄ -P	0.334***	0.416***	0.621***	0.452**	0.491**	0.401**	
SR	0.349***	0.498***	0.375***	0.323**	0.429**	0.243*	
DHA	0.463***	0.525***	0.416***	0.507**	0.492**	0.366**	
K ₁₂	0.704***	0.671***	0.907***	0.630***	0.563***	0.690***	

Significant at *, p < 0.05, **, p < 0.01, p < 0.001, NS, not significant (p > 0.05) K_{12} , litter decomposition rate constant at 12 months.

brought about greater soil arthropod abundance in shaded systems than in the open ones (Faminow and Rodriguez, 2001). However, decreased litter quantity/substrate, the onset of summer and a corresponding decrease in soil moisture and warmer temperatures towards June, affected abundance of soil fauna at the 8th and 12th months of samplings. Changes in soil and litter moisture induce changes within functional groups or shift the balance between different functional groups in the soil decomposer community, affecting litter decomposition (Swift et al., 1998). The highest decomposition rate and densest population of soil arthropods during the wet season (monsoon) is similar to the observation of Schowalter et al. (1991). The highest faunal abundance in TLS litter than other litters suggested that *L. sindicus* litter was a better substrate that attracted soil fauna to a greater extent. However, changes in abundance and activity of soil invertebrates also depend upon litter chemistry (Zimmer and Topp, 2002; Schädler and Brandl, 2005b) and microhabitats. This was indicated by the highest faunal abundance in the 3-7 cm soil layer. This showed that soil fauna associated with litter decomposition preferred niches under the tree canopy.

4.3. Decomposition-induced changes in soil nutrients

An improvement in soil nutrient status was seen from the 1.5-3 fold increase in the concentrations of SOC, TN, NH₄-N, NO₃-N and PO₄-P at the 12th month of sampling than at the start of the experiment. Although the highest rate of litter decomposition was at 4 months, the decomposition and mineralization allowed the release of soil nutrients resulting in an increase in the value of these soil variables at the end of the year (Thomas and Prescott, 2000). Coleman et al. (1992) documented that bacteria and fungi produce soil organic matter from waste products and thus increase the level of organic carbon in soil. Quality of litter and associated faunal abundance improved SOC and available nutrients in the mixture of tree and grass litters, than in T litter alone (Figs. 2–4). This is supported by a positive correlation (r = 0.523, p < 0.01) between soil nutrients and faunal abundance. Increased rates of nutrient mineralization suggested a rapid recycling of organic matter and a greater amount of nutrients available under increased soil faunal abundance. Many workers (Maity and Joy, 1999; Kumar et al., 1999; Frouz, 2008; Warren and Zou, 2002) observed higher nutrient status and biological activities associated with abundance and biomass of soil fauna. Here mixed litters and corresponding greater volume of litter decomposition through soil biota, available under the canopy, enhanced concentrations of soil nutrients. Ashwini and Sridhar (2004) also observed highest soil moisture, organic carbon, phosphate, potassium, calcium and magnesium when abundance and biomass of millipedes was high. Relatively high concentrations of soil nutrients in the 3-7 cm soil layer were positively related to faunal abundance and decomposition rate. It reflected the facilitative role of soil fauna in improving microbial growth and soil health. Greater soil respiration (an indicator of microbial population) in the 3–7 cm soil layer caused a reduction in soil organic carbon. Pramanik et al. (2001) studied nutrient mobilization from leaf litter by detritivore soil arthropods and found a corresponding release of organic carbon and nitrates.

4.4. Decomposition-induced biochemical changes

Litter quality and micro-climate influenced biochemical (soil respiration and dehydrogenase) properties, which were greater in the mixed litter, under the tree canopy and in the 3–7 cm soil layer as compared to T litter alone, outside the tree canopy and other soil layers, respectively. However, the effects of soil fauna, which fragment litter and facilitate decomposition and microbial growth,

cannot be ruled out. The highest litter decomposition and consequent microbial growth during July to October enhanced SR and DHA by 2- to 3-fold than their initial values in June 2004. Thus litter decomposed soil became biologically more active, particularly in mixed litter placed inside the canopy than outside the canopy, as indicated by increased level of dehydrogenase activity (Ciarkowska1 and Gambuoe, 2005; Tripathi et al., 2008). However. a decrease in substrate/litter quantity, faunal abundance and reduced microbial growth with advancement of summer decreased soil respiration and dehydrogenase activities after 8 and 12 months of litter decomposition (Fig. 4). Other studies also suggest that the soil respiration is influenced by the availability of carbon substrate for the microbial population (Seto and Yanagiya, 1983), the soil biota population (Singh and Shukla, 1977; Rai and Srivastava, 1981), soil physical and chemical properties (Boudot et al., 1986) and soil drainage (Luken and Billings, 1985; Freeman et al., 1993). Differences in soil respiration rate between canopy zones illustrated a conducive microclimate under the C. mopane canopy allowing growth of the microflora (Raich and Potter, 1995). Dehydrogenase activity appeared to be more related to the metabolic state of the microbial population of the soil than to the activity of free enzymes acting on a particular substrate. Soil moisture and temperature during July to October was advantageous to growth of microorganisms and soil fauna and resulted in the highest dehydrogenase activity. Rao and Venkateswarlu (1993) observed higher populations of different microorganisms during July-August but the study of Sasson (1972) indicated that higher temperatures and soil drving during summer months affected microbial populations in an arid environment. The lowest DHA was recorded in winter in the present study, indicating that the microorganisms remained in a state of biochemical inactivity, as also found by Milosevic (1988). A positive relation of litter associated soil fauna with soil respiration and dehydrogenase activity demonstrated the influence of faunainduced biotic activities. However, better substrate (mixed litter TLS) and greater growth of both soil fauna and microbes (indicated by increased DHA and soil health) under tree canopy and in the 3–7 cm soil layer indicate the importance of microhabitat and litter quality in litter decomposition and nutrient release (Kizilkaya, 2008; Wall et al., 2008).

5. Conclusions and recommendations

In this study soil nutrients and soil biochemical properties were enhanced by increased litter decomposition rates, driven by microclimate and soil fauna in this desert ecosystem. Here, the integration of *C. mopane* trees in *L. sindicus* pastureland promoted this, through increased decomposition rates and soil fertility and functionality. This demonstrated the beneficial effects of canopy coverage and soil fauna on the functional aspects of soil. Applications such as this to silvopasture systems may help improve soil fertility and sustain productivity in hot arid landscapes.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http:// dx.doi.org/10.1016/j.actao.2013.01.013.

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