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Original article

Seasonal abundance and activity of pill millipedes (*Arthrosphaera magna*) in mixed plantation and semi-evergreen forest of southern India

Krishna M. Ashwini, Kandikere R. Sridhar *

Microbiology and Biotechnology, Department of Biosciences, Mangalore University, Mangalagangotri, Mangalore 574 199, Karnataka, India

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Abstract

Seasonal occurrence and activity of endemic pill millipedes (*Arthrosphaera magna*) were examined in organically managed mixed plantation and semi-evergreen forest reserve in southwest India between November 1996 and September 1998. Abundance and biomass of millipedes were highest in both habitats during monsoon season. Soil moisture, conductivity, organic carbon, phosphate, potassium, calcium and magnesium were higher in plantation than in forest. Millipede abundance and biomass were about 12 and 7 times higher in plantation than in forest, respectively ($P < 0.001$). Their biomass increased during post-monsoon, summer and monsoon in the plantation ($P < 0.001$), but not in forest ($P > 0.05$). Millipede abundance and biomass were positively correlated with rainfall ($P = 0.01$). Besides rainfall, millipedes in plantation were positively correlated with soil moisture as well as temperature ($P = 0.001$). Among the associated fauna with pill millipedes, earthworms rank first followed by soil bugs in both habitats. Since pill millipedes are sensitive to narrow ecological changes, the organic farming strategies followed in mixed plantation and commonly practiced in South India seem not deleterious for the endangered pill millipedes *Arthrosphaera* and reduce the risk of local extinctions.

Keywords: Saprophagous fauna; Pill millipedes; *Arthrosphaera magna*; Mixed plantation; Semi-evergreen forest

1. Introduction

Among saprophagous macrofauna, millipedes, earthworms, woodlice and slugs are of considerable value in soil humification (Anderson et al., 1983; Morgan et al., 1989). Richness and diversity of saprophagous fauna are influenced by a wide range of landuse, agricultural, forestry and wildlife conservation practices (Curry, 1994; Didham et al., 1996; Edwards and Bohlen, 1995; Wardle, 1995). Climate and litter chemistry are the most important factors regulating the rates of organic matter decomposition affecting decomposers and saprophagous invertebrates (Aerts, 1997; Meentenmeyer, 1978).

Pill millipedes belonging to the genus *Arthrosphaera* (Order: Sphaerotheriidae) are endemic to southern India and Sri Lanka (Achar, 1986; Achar, 1987; Attems, 1936; Pocock, 1899) and within this genus, *Arthrosphaera magna* Attems (Attems, 1936) was found to be very abundant in organically managed mixed plantation of southern India (Ashwini, 2003; Ashwini, 2002). They can also be found in forests but not in chemically managed plantations. Previous studies revealed that Julid pill millipede richness was high in natural heterogeneous woodlands than in homogeneous plantations (Dangerfield, 1990; Dangerfield and Telford, 1992). However, similar information is lacking on endemic pill millipedes *Arthrosphaera*. Thus, the specific objectives of the current study were to investigate seasonal occurrence of two abundant saprophagous invertebrates, earthworms in general and the pill millipedes *A. magna* in relation to soil edaphic factors and climatic features in a mixed plantation and a semi-evergreen forest reserve of southern India. In addition, mixed plantation land use practices that enhanced the abundance of *A. magna* have been documented.

2. Materials and methods

The survey was carried out for 2 consecutive years from November 1996 to September 1998. The area surveyed

* Corresponding author. Fax: +91 824 2287 367.
E-mail address: sirikr@yahoo.com (K.R. Sridhar).

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(12°42′N, 75°E) receives precipitation up to 390 cm per annum, most of it occurs during southwest monsoon (June–September). Atmospheric temperature fluctuates between 23 and 33 °C, while relative humidity between 84 and 96%. Rainfall data were obtained from the meteorological records of Central Plantation Crops Research Institute, Vittal, Karnataka State, located about 10 km away from the study sites.

2.1. Study sites

Our two study sites include a mixed plantation and an adjacent forest reserve. The plantation (1 ha) is about 30-year-old and the crops cultivated include: areca (*Areca catechu*), cocoa (*Theobroma cacao*), banana (*Musa paradisiaca*) and coconut (*Cocos nucifera*). During post-monsoon season (October), each tree basin receives 20 kg organic manure (3 months composted coconut coir pith, coffee husk and poultry manure, 2:2:1 ratio, w/w) and 10 kg farmyard manure (leaf litter and green leaves seasoned at cattle shed up to 2 months with urine and dung). In addition, leaf litter generated from the plantation was heaped at the basin. Plantation receives irrigation through sprinklers (equivalent to 2.5 cm rain) from December through May. The interspaces do not receive organic manure, but receive uniform sprinkling of water. The canopy cover of plantation partially allows sunlight. The soil texture of plantation is categorized as sandy loam (Kanwar and Chopra, 1981).

The semi-evergreen forest reserve (6 ha) is located adjacent to the mixed plantation. This forest has thick canopy, possesses a large amount of litter on the floor and devoid of human interference. The texture of soil is sandy loam. The major tree species of the forest include: *Acacia auriculiformis*, *Cinnamomum malabatrum*, *Dalbergia latifolia*, *Entanda* sp., *Holigarna ferruginea*, *Lagerstroemia microcarpa*, *Mangifera indica*, *Mimusops elengi*, *Piper* spp., *Sapium* sp., *Syzygium caryophyllatum*, *Terminalia chebula* and *Ziziphus mauritiana*.

2.2. Population density

Sampling of *A. magna* was performed every 2 months from November 1996 to September 1998 in the plantation and the forest. Five replicate samples on each occasion from each site were randomly collected. In the plantation, sampling was restricted to one sample per tree basin, whereas in the forest, one sample per plant was collected at a distance of 1–2 m away from tree base. Macrofauna was sampled by forcing steel frames (30 × 30 × 30 cm) into the soil, excavated soil along with litter (27,000 cm^3) was transferred to trays. Biomasses (fresh weight) of millipedes (*A. magna*, non-*Arthrosphaera* spp.) and earthworms were determined to the nearest 0.01 g on the sampling spot (Mettler Toledo, Switzerland; Model PB 303DR). The epigeic (litter-dwelling) and endogeic (soil-dwelling) macrofauna were enumerated. As ants and termites were numerous, number of colonies per sample was recorded.

2.3. Soil analysis

All soil parameters were assessed using the soil excavated for faunal observation. Soil samples were weighed, oven-dried at 80 °C up to 24 h and reweighed to determine the moisture gravimetrically. Soil temperature was measured by mercury thermometer at a depth of 15 cm in each sampling point. Soil and distilled water were mixed (1:2.5, w/v), shaken (15 min) and pH was detected using pH meter (Systronics, India; Model 335). The soil–water suspension prepared for pH determination was used to measure conductivity (Systronics, India; Model 304). Walkley and Black's rapid titration method was employed to quantify the organic carbon in soil (Jackson, 1973). Available phosphorus was determined spectrophotometrically (Systronics, India; Model 106) based on the method outlined by Jackson (Jackson, 1973). Available potassium was detected using flame photometer (Systronics, India; Make MK1/MK3) (Jackson, 1973). Exchangeable calcium and magnesium were determined based on Versenate method (Jackson, 1973).

2.4. Statistical analysis

Difference in the biomass of *A. magna* of plantation and forest was assessed by paired *t*-test and one-way ANOVA was employed to assess the difference in biomass of *Arthrosphaera* during post-monsoon, summer and monsoon seasons in plantation and forest (Stat Soft Inc., 1995). Pearson correlation was used to investigate the relationship between millipede abundance and biomass vs. climatic and soil edaphic features (Stat Soft Inc., 1995). Difference in soil edaphic features between plantation and forest was evaluated by paired *t*-test (Stat Soft Inc., 1995).

3. Results

Rainfall and soil temperature were seasonal with rain occurring during June–December (maximum in July) (Fig. 1). Soil temperature fluctuated between 23 °C (November) and 29 °C (June). Table 1 reveals the seasonal fluctuations of soil edaphic features. Soil moisture, conductivity, organic carbon, phosphate, potassium, calcium and magnesium were higher at plantation than forest. Soil pH was more acidic in forest (5.8) than in plantation (6.3).

Abundance of pill millipedes in mixed plantation was highest during September 1997, while biomass during July 1997 (Fig. 2). They were significantly more abundant and had a higher biomass in the plantation ($P < 0.05$) than in the forest ($P > 0.05$). Millipede biomass was also significantly differed during post-monsoon, summer and monsoon seasons in the plantation ($P < 0.001$), but not in the forest ($P > 0.05$). In the forest, maximum of 2.2 individuals were seen per sample, while in plantation the values reached up to 26.2 (Fig. 2). Values for highest biomass in forest and plantation were 9.1 vs. 66.6 g per sample. Millipede abundance as well as

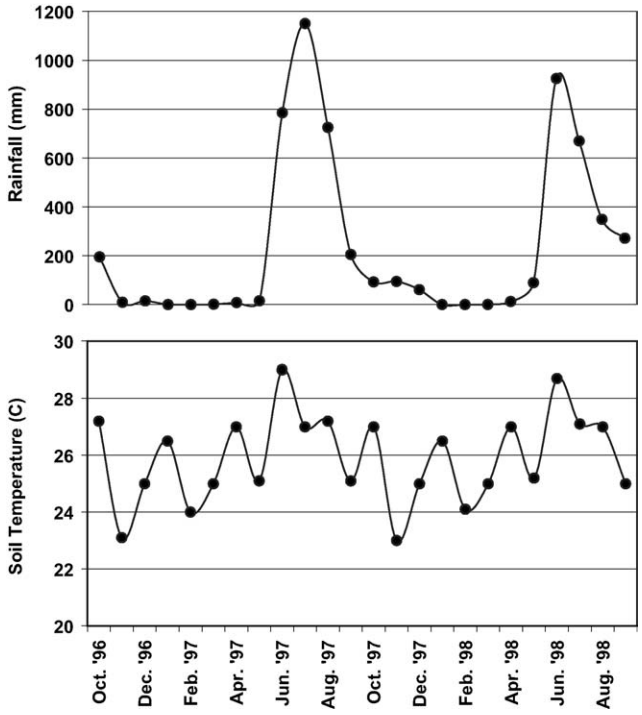

Fig. 1. Seasonal fluctuations in rainfall and soil temperature at study location.

biomass of plantation were positively correlated ($P = 0.001$) with rainfall, soil moisture and soil temperature. Abundance was positively correlated with soil phosphate ($P = 0.01$) and biomass with calcium ($P = 0.01$). Biomass of millipedes in plantation was negatively correlated with soil pH ($P = 0.01$) and potassium ($P = 0.05$). In the forest, a significant positive correlation ($P = 0.01$) was observed between millipede (abundance and biomass) and rainfall. In forest, abundance was negatively correlated with soil magnesium ($P = 0.05$). Paired *t*-test revealed significant difference in soil edaphic features between plantation and forest ($P < 0.001$).

The second most abundant group in soil samples was earthworms. Their abundance as well as biomass was highest during March 1997 in plantation and September 1998 in forest (Fig. 3). Pill millipedes, other millipedes, earthworms and soil bugs were dominant in both the plantation and the forest. In the plantation, centipedes were also abundant, whereas in the forest snails and ants were also numerically important (Table 2 and Fig. 4).

4. Discussion

Chemical fertilizers and pesticides are detrimental to soil saprophagous fauna and in turn deteriorate the soil qualities. Agricultural practices such as ploughing, cultivation of

Table 1
Seasonal fluctuations of soil physicochemical features of plantation and forest reserve surveyed for pill millipedes (*A. magna*) ($N = 5$; mean ± S.D.)

Month	Site	Moisture (%)	pH	Conductivity (m mhos cm^{-1})	Organic carbon (%)	Phosphate (μg g^{-1})	Potassium (mg g^{-1})	Calcium (mg g^{-1})	Magnesium (mg g^{-1})
November 1996	Plantation	47.6 ± 2.9	6.30 ± 0.12	0.29 ± 0.04	4.2 ± 0.4	41.00 ± 1.0	0.37 ± 0.01	2.19 ± 0.14	0.80 ± 0.02
	Forest	27.7 ± 0.9	5.84 ± 0.05	0.22 ± 0.01	3.3 ± 0.2	9.43 ± 0.32	0.13 ± 0.01	1.95 ± 0.06	0.69 ± 0.02
January 1997	Plantation	41.4 ± 1.6	6.24 ± 0.05	0.35 ± 0.04	4.1 ± 0.3	45.0 ± 1.90	0.33 ± 0.03	2.16 ± 0.13	0.83 ± 0.01
	Forest	18.5 ± 0.4	5.88 ± 0.05	0.22 ± 0.01	3.0 ± 0.1	10.47 ± 0.7	0.18 ± 0.02	1.92 ± 0.01	0.71 ± 0.01
March 1997	Plantation	41.0 ± 1.9	6.30 ± 0.10	0.30 ± 0.02	3.6 ± 0.1	49.70 ± 1.3	0.30 ± 0.02	2.60 ± 0.11	0.84 ± 0.02
	Forest	18.2 ± 0.5	5.88 ± 0.04	0.22 ± 0.01	2.9 ± 0.4	13.56 ± 0.6	0.15 ± 0.01	2.01 ± 0.04	0.74 ± 0.02
May 1997	Plantation	39.6 ± 1.0	6.40 ± 0.10	0.39 ± 0.01	4.0 ± 0.2	63.10 ± 3.3	0.39 ± 0.003	2.87 ± 0.19	0.91 ± 0.05
	Forest	18.6 ± 0.3	5.78 ± 0.11	0.30 ± 0.01	2.8 ± 0.2	14.20 ± 0.5	0.13 ± 0.01	1.98 ± 0.04	0.71 ± 0.03
July 1997	Plantation	74.1 ± 2.2	6.00 ± 0.10	0.20 ± 0.01	4.1 ± 0.4	46.10 ± 2.2	0.24 ± 0.04	3.01 ± 0.07	0.81 ± 0.05
	Forest	43.5 ± 1.0	5.56 ± 0.09	0.27 ± 0.01	1.7 ± 0.1	13.70 ± 0.7	0.10 ± 0.004	2.20 ± 0.23	0.67 ± 0.04
September 1997	Plantation	66.0 ± 2.7	6.60 ± 0.10	0.35 ± 0.02	4.5 ± 0.2	61.80 ± 9.4	0.21 ± 0.01	2.59 ± 0.08	0.75 ± 0.05
	Forest	30.9 ± 0.9	5.62 ± 0.04	0.20 ± 0.01	2.7 ± 0.1	15.80 ± 2.7	0.14 ± 0.01	2.03 ± 0.11	0.68 ± 0.05
November 1997	Plantation	54.1 ± 1.5	6.50 ± 0.10	0.32 ± 0.02	5.2 ± 0.4	45.30 ± 0.9	0.23 ± 0.02	1.88 ± 0.06	0.74 ± 0.04
	Forest	29.0 ± 0.7	5.84 ± 0.05	0.21 ± 0.01	2.8 ± 0.1	12.5 ± 0.83	0.12 ± 0.01	1.90 ± 0.08	0.67 ± 0.04
January 1998	Plantation	41.2 ± 2.2	6.42 ± 0.04	0.33 ± 0.10	5.5 ± 0.3	40.8 ± 1.10	0.22 ± 0.01	1.97 ± 0.13	0.81 ± 0.03
	Forest	18.4 ± 0.9	5.96 ± 0.09	0.23 ± 0.01	3.1 ± 0.2	9.86 ± 1.77	0.15 ± 0.01	1.86 ± 0.14	0.74 ± 0.03
March 1998	Plantation	43.5 ± 2.1	6.50 ± 0.10	0.32 ± 0.02	4.9 ± 0.1	45.10 ± 3.3	0.33 ± 0.06	2.24 ± 0.28	0.86 ± 0.03
	Forest	17.3 ± 0.4	5.92 ± 0.08	0.22 ± 0.01	3.2 ± 0.4	13.84 ± 0.7	0.14 ± 0.01	1.82 ± 0.08	0.74 ± 0.02
May 1998	Plantation	55.8 ± 2.0	6.30 ± 0.10	0.50 ± 0.01	4.5 ± 0.5	69.80 ± 5.9	0.41 ± 0.01	2.75 ± 0.40	0.91 ± 0.04
	Forest	33.3 ± 1.3	5.72 ± 0.08	0.31 ± 0.01	2.8 ± 0.1	14.14 ± 0.2	0.16 ± 0.001	1.75 ± 0.12	0.71 ± 0.01
July 1998	Plantation	45.8 ± 2.7	6.10 ± 0.10	0.23 ± 0.04	4.8 ± 0.3	54.0 ± 3.70	0.20 ± 0.003	2.38 ± 0.29	0.81 ± 0.05
	Forest	30.5 ± 0.7	5.64 ± 0.09	0.27 ± 0.02	2.9 ± 0.1	13.44 ± 0.9	0.10 ± 0.004	1.58 ± 0.03	0.63 ± 0.02
September 1998	Plantation	60.6 ± 1.5	6.44 ± 0.05	0.27 ± 0.02	4.2 ± 0.4	36.70 ± 2.3	0.31 ± 0.02	1.92 ± 0.17	0.68 ± 0.03
	Forest	29.6 ± 1.3	5.88 ± 0.08	0.19 ± 0.01	2.9 ± 0.1	8.99 ± 0.61	0.12 ± 0.01	1.99 ± 0.08	0.68 ± 0.03
Mean ± S.D.	Plantation	51.4 ± 12	6.34 ± 0.17	0.32 ± 0.08	4.5 ± 0.6	49.80 ± 10.2	0.30 ± 0.07	2.38 ± 0.38	0.81 ± 0.07
	Forest	26.3 ± 8.2	5.79 ± 0.13	0.24 ± 0.04	2.9 ± 0.4	12.49 ± 2.23	0.13 ± 0.03	1.92 ± 0.16	0.70 ± 0.03
Range	Plantation	39.6 – 74.1	6.00–6.60	0.20–0.50	3.6–5.5	36.70–69.8	0.2–0.41	1.88–3.01	0.68–0.91
	Forest	17.3 – 43.5	5.56–5.96	0.19–0.31	1.7–3.3	8.99–15.80	0.1–0.18	1.58–2.2	0.63–0.74

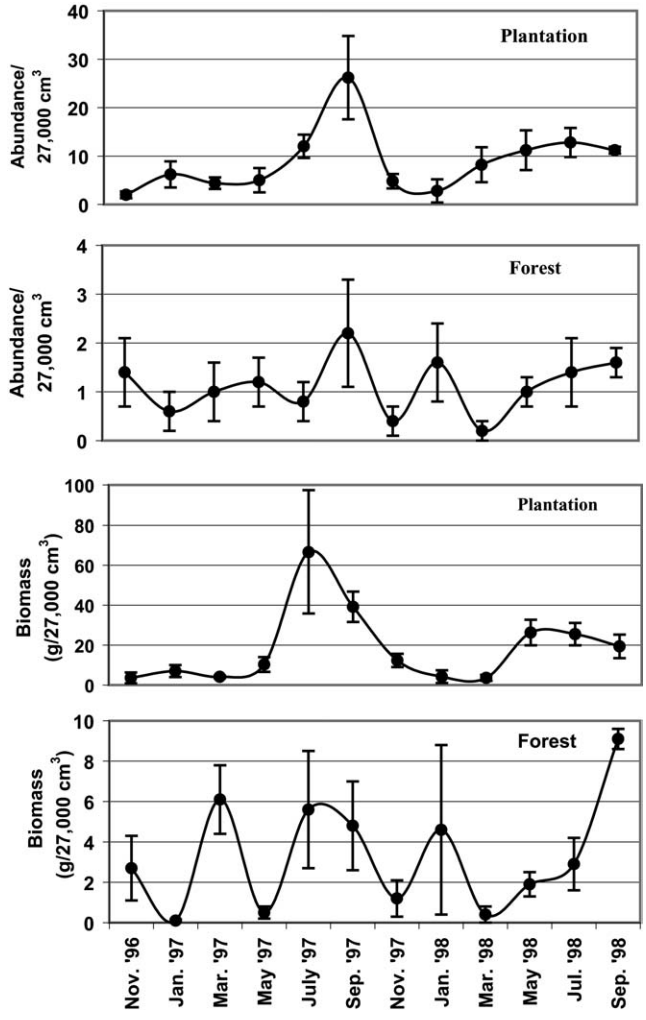

Fig. 2. Seasonal fluctuations in abundance and biomass of *A. magna* in a mixed plantation and a forest reserve ($N = 5$ + S.D.).

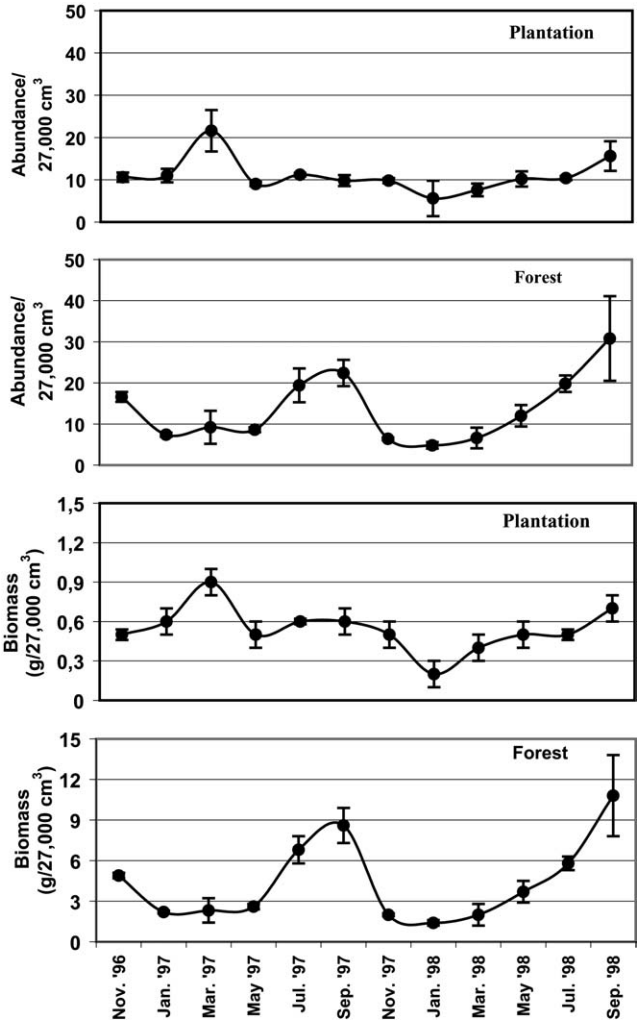

Fig. 3. Seasonal fluctuations in abundance and biomass of earthworms in a mixed plantation and a forest reserve ($N = 5$ + S.D.).

monocrops and application of pesticides have beneficial (Edwards and Lofty, 1969; Raw, 1967) as well as adverse (Cook et al., 1979; Perfect et al., 1981) impacts on specific species of soil fauna. Organic farming can be considered as a viable strategy to maintain the soil fertility for sustainable agriculture. Exclusive organic farming practices in a mixed plantation in southern India (Varanashi Farms, Adyanadka, Dakshina Kannada, Karnataka) over a decade had a profound influence on the diversity of saprophagous fauna (Ashwini, 2003; Ashwini, 2002). Organic farming practices followed in mixed plantation include: 1) utilization of coffee husk, coconut husk, coconut husk and poultry manure through composting (the former two pollute aquatic habitats due to high phenolics); 2) use of farmyard manure; 3) addition of organic matter to basins in heaps; 4) lack of tilling and plowing of floor; 5) addition of leaf litter and green manure to basins twice a year; 6) no weeding, instead weeds above the ground were chopped and used as green manure; 7) intermittent irrigation through sprinklers during post-monsoon and summer seasons. These practices resulted in the accumulation of organic matter at the bases of trees, creating favorable conditions for saprophagous fauna.

Table 2
Occurrence of fauna in association with pill millipedes (*A. magna*) in plantation and forest reserve (% out of 60 samples)

Fauna	Plantation	Forest
Pill millipedes	91.7	58.3
Other millipedes	50.0	65.0
Earthworms	100	100
Centipedes	56.7	33.3
Soil bugs	81.7	98.3
Coleopteran larvae	5.0	6.7
Beetles	5.0	3.3
Spiders	8.3	40.0
Cockroaches	8.3	15.0
Snails	35.0	58.3
Ants	43.3	50.0
Termites	20.0	28.3
Springtails	33.3	13.3
Insect larvae	16.7	25.0
Caterpillars	3.3	13.3
Scorpions	1.7	1.7

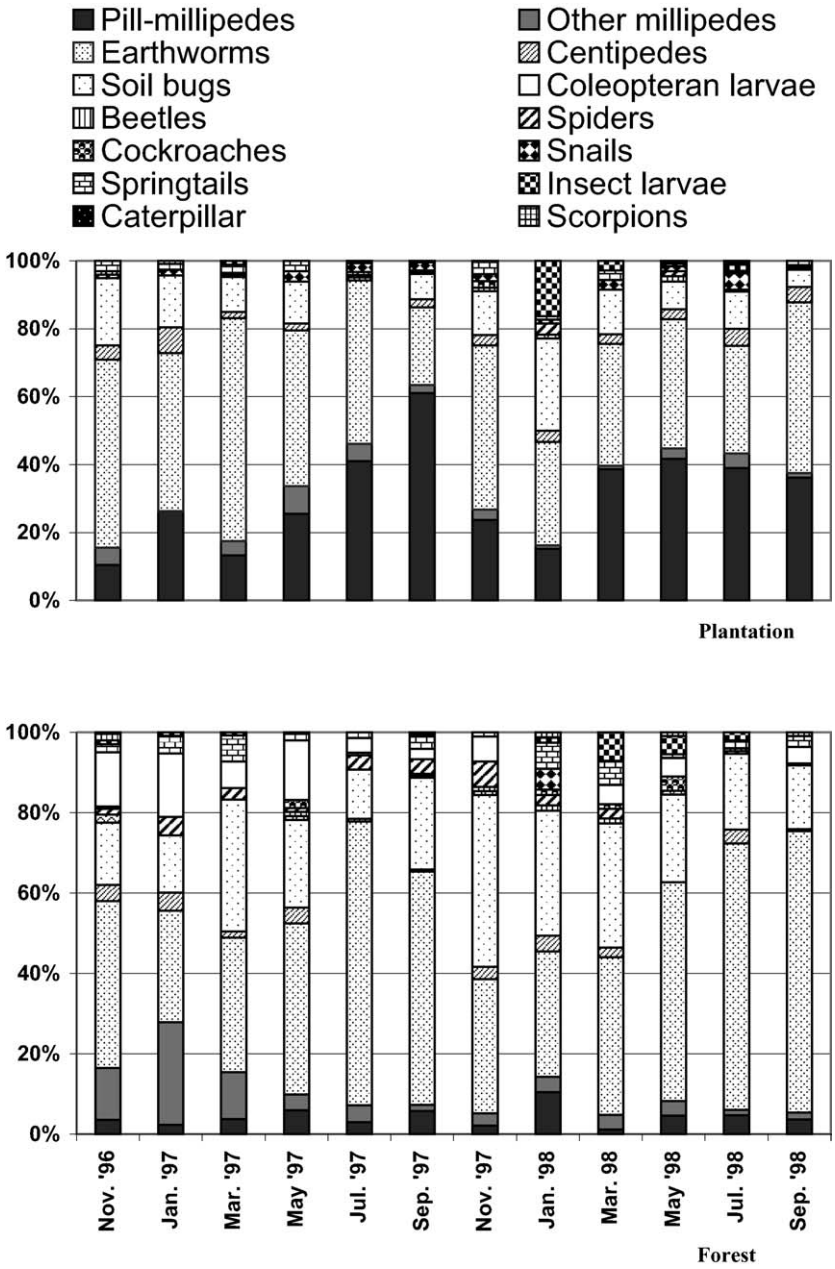

Fig. 4. Seasonal fluctuations of fauna associated with pill millipedes (*A. magna*) in a mixed plantation and a forest reserve.

According to Dangerfield et al. (1992), millipedes with large body size possess high tolerance to dry conditions and exhibit extended periods of surface activity. Such features of millipedes are linked for the search of high quality food sources, mate acquisition and avoidance of saturated soil conditions (Dangerfield et al., 1992). Earlier observation (Ashwini, 2003) revealed that adult *A. magna* in mixed plantation were active for 7 months (early or late June–January), while juveniles emerge during late July or early August, active for about 4 months and hibernates prior to adults in November. In forest, adults were active for 5 months (July–November), while activity of young ones restricted to 4 months (August–November) possibly due to decline of soil moisture (Table 1). Warren and Zou (2002) indicated that millipedes are sensitive to litter chemistry at narrow spatial scales (meters to decameters), while earthworms at higher order of soil physical conditions. Our study also reflects such phenomenon in terms of pill millipede biomass were important in mixed plantation, while earthworms were more important in the forest. Endogeic earthworms attracted towards the fecal pellets of millipedes and incorporated them into soil (Bonkowski et al., 1998). Duel inoculation of millipedes (*Glomeris marginata*) and earthworms (*Octolasion lacteum*) resulted in significant increase in breakdown of beech litter and improved the soil fertility (Bonkowski et al., 1998). Earthworms (*Lumbricus castaneus* and *O. lacteum*) incorporated the fecal pellets of

millipede (*G. marginata*) into soil and elevated carbon mineralization of pellets within 14 days (Scheu and Wolters, 1991).

The major objective of sustainable farming is to achieve long-term benefits with minimum adverse effects on the environment. Plantation practices without fragmentation would bring more benefits as fragmentation severely affects biodiversity and conservation of wildlife. Small-scale variation in structure of vegetation, leaf litter fall and soil fertility in natural Miombo woodland, Zimbabwe exhibited significant heterogeneity in composition and abundance of soil fauna (Dangerfield, 1990). Long-term intra-site heterogeneity in organic matter facilitated the invasion, survival and activity of *A. magna* in mixed plantation in our study warrants following such practices to support sensitive saprophagous fauna like *Arthrosphaera* in plantations. *Arthrosphaera* are the indicators of restoration of soil quality as they are sensitive to narrow ecological fluctuations (Kime and Golovatch, 2000). The current study revealed the possibilities of rehabilitation of plantations with precise organic farming practices to enhance the *A. magna* population and in turn other saprophagous fauna in southern Indian climatic conditions. Exclusive organic farming, minimum disturbance, no tillage and minimum weeding are the common practices employed in mixed plantation.

It has been predicted that *A. magna* might have invaded plantations by the adjacent forest reserve and active in plantation for extended periods due to elevated organic matter, which conserve moisture in soil. As *Arthrosphaera* are endemic, their invasion from forest to mixed plantations might reduce the risks of local extinction. To understand the population dynamics and activities of the pill millipede *A. magna* in relation to edaphic factors, manipulative studies by organically enriching some sections of natural semi-evergreen forest reserve during different seasons with varying water regimes are underway in our school.

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References

Achar, K.P., 1986. Analysis of male meiosis in seven species of Indian pill-millipede (Diplopoda: Myriapoda). Caryologia 39, 89–101.

Achar, K.P., 1987. Chromosomal evolution in Diplopoda (Myriapoda: Arthropoda). Caryologia 40, 145–155.

Anderson, J.M., Ineson, P., Huish, S.A., 1983. Nitrogen and cation mobilization by soil fauna feeding on leaf litter and soil organic matter from deciduous woodlands. Soil Biol. Biochem. 15, 463–467.

Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79, 439–449.

Ashwini, K.M., 2003. Ecological Studies on Indian Pill Millipede, *Arthrosphaera magna*, Ph.D. Thesis, Mangalore University, India.

Ashwini, K.M., Sridhar, K.R., 2002. Towards organic farming with millipede—*Arthrosphaera magna*. Current Science 82, 20–22.

Attems, C., 1936. Memoirs of the Indian Museum 11, 133–167.

Bonkowski, M., Scheu, S., Schaefer, M., 1998. Interactions of earthworms (*Octolasion lacteum*), millipedes (*Glomeris marginata*) and plants (*Hordelymus europaeus*) in a beech wood on a basalt hill: implications for litter decomposition and soil formation. Appl. Soil Ecol. 9, 161–166.

Cook, A.G., Critchley, B.R., Critchley, V., Perfect, T.J., Russell-Smith, A., Yendon, R., 1979. The effects of soil treatment with DDT on the biology of a cultivated forest soil in the sub-humid tropics. Pedobiologia 19, 279–292.

Curry, J.P., 1994. Grassland Invertebrates: Ecology, Influence on Soil Fertility and Effects on Plant Growth. Chapman and Hall, London.

Dangerfield, J.M., 1990. Abundance, biomass and diversity of soil macrofauna in savanna woodland and associated managed habitats. Pedobiologia 34, 141–150.

Dangerfield, J.M., Telford, S.R., 1992. Species diversity of Julid millipedes: between habitat comparisons within the seasonal tropics. Pedobiologia 36, 321–329.

Dangerfield, J.M., Milner, A.E., Mathews, R., 1992. Seasonal activity pattern and behaviour of juliform millipedes in south-eastern Botswana. J. Tropical Ecol. 8, 451–464.

Didham, R.K., Ghazoul, J., Stork, N.E., Davis, A.J., 1996. Insects in fragmented forests. TREE 11, 255–260.

Edwards, C.A., Bohlen, P.J., 1995. Biology of Earthworms. Chapman and Hall, New York.

Edwards, C.A., Lofty, J.R., 1969. The influence of agricultural practice on soil macroarthropod populations. In: Sheals, J.G. (Ed.), The Soil Ecosystem. Systematic Association, London, pp. 237–247.

Jackson, M.L., 1973. Soil Chemical Analysis. Prentice-Hall International, USA.

Kanwar, S.L., Chopra, J.S., 1981. Analytical Agricultural Chemistry. Kalyani Publishers, New Delhi, India.

Kime, R.D., Golovatch, S.I., 2000. Trends in the ecological strategies and evolution of millipedes (Diplopoda). Biol. J. Linn. Soc. 69, 333–349.

Meentenmeyer, V., 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59, 465–472.

Morgan, C.R., Schindler, S.C., Mitchell, M.J., 1989. The effects of feeding by *Oniscus osellus* (Isopoda) on nutrient cycling in an incubated hardwood forest soil. Biol. Fert. Soils 7, 239–246.

Perfect, T.J., Cook, A.G., Critchley, B.R., Russell-Smith, A., 1981. The effect of crop protection with DDT on the macroarthropod population of a cultivated forest soil in the sub-humid tropics. Pedobiologia 21, 7–18.

Pocock, R.I., 1899. A monograph of the pill-millipedes (Zephroniidae) inhabiting India, Cylon and Burma. J. Bombay Nat. Hist. Soc. 12, 269–285.

Raw, F., 1967. Arthropods (except Acari and Collembola. In: Burges, N., Raw, J. (Eds.), Soil Biology. Academic Press, London, pp. 323–362.

Scheu, S., Wolters, V., 1991. Influence of fragmentation and bioturbation on the decomposition of ^{14}C-labelled beech leaf litter. Soil Biol. Biochem. 23, 1029–1034.

Stat Soft Inc, 1995. STATISTICA for Windows. Stat Soft Inc., Tulsa, OK, USA.

Warren, M.W., Zou, X., 2002. Soil macrofauna and litter nutrients in three tropical tree plantations on a disturbed site in Puerto Rico. Forest Ecology and Management 170, 161–171.

Wardle, D.A., 1995. Impact of disturbance on detritus food webs in agroecosystems of contrasting tillage and weed management practices. Adv. Ecol. Res. 26, 105–185.